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COMPARING CONVENTIONAL AND NONINVASIVE MONITORING  
TECHNIQUES FOR ASSESSING COUGAR POPULATION SIZE IN  
THE SOUTHERN GREATER YELLOWSTONE ECOSYSTEM

by

Peter D. Alexander

A thesis submitted in partial fulfillment  
of the requirements for the degree

of

MASTER OF SCIENCE

in

Wildlife Biology

Approved:

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UTAH STATE UNIVERSITY  
Logan, Utah

2016

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## ABSTRACT

Comparing Conventional and Noninvasive Monitoring Techniques for Assessing  
Cougar Population Size in the Southern Greater Yellowstone Ecosystem

by

Peter D. Alexander, Master of Science

Utah State University, 2016

Major Professor: Dr. Eric M. Gese  
Department: Wildland Resources

Cougars (*Puma concolor*) are difficult to census due to their large home ranges, low densities, and cryptic nature. The conventional “gold-standard” method for estimating cougar abundance entails the capture and radio-tagging of individuals in a study area in an attempt to acquire a direct enumeration of animals in the population. While this method provides an accurate abundance estimate, it is logistically challenging and prohibitively expensive. Noninvasive survey techniques may offer the ability to both accurately and inexpensively monitor cougar populations. While noninvasive techniques have been used on cougar populations, there remain questions on their accuracy and comparative efficacy. We estimated the density of a cougar population in Northwest Wyoming using direct enumeration, and used this estimate as a reference with which to evaluate the accuracy and cost-effectiveness of three types of noninvasive surveys performed between 2010 and 2014. The noninvasive methods included two annual mark-

recapture sessions of: 1) remote camera trapping, 2) winter hair-collection transects, and 3) scat detection dog surveys.

We GPS tracked 13 adult cougars (males = 5, females = 8) over 3 annual periods (Sep 2010 – Sep 2013). We used proportional home range overlap to determine density in a 1,570 km<sup>2</sup> area. The average density was 0.82 cougars/100 km<sup>2</sup> ( $\pm$  0.10 SD; n = 3 years). The remote camera surveys produced a mean density of 0.60 cougars/100 km<sup>2</sup> (n = 2 years; relative SD = 56.5%). The scat detection dog surveys produced an average density of 2.41 cougars/100 km<sup>2</sup> (n = 2 years; relative SD = 12.6%). The winter transects failed to produce a sample size large enough for an abundance estimate. Due to the inclusion of non-adults in the scat sampling, and the fact that the reference estimate was essentially a minimum count of adults, we believe that the scat-based estimate was more accurate than the lower estimate produced by remote cameras. Additional analysis indicated that individual identification of cougars in photographs may not be reliable, challenging the validity of photo-based abundance estimates of cougars. On a cost-per-detection basis, scat detection dogs were the most cost effective method (scat detection dogs = \$341; remote cameras = \$3,241; winter transects = \$7,627).

(160 pages)

## PUBLIC ABSTRACT

Comparing Conventional and Noninvasive Monitoring Techniques for Assessing  
Cougar Population Size in the Southern Greater Yellowstone Ecosystem

by

Peter D. Alexander

Determining the abundance or density of wildlife populations is needed for informed decision-making by wildlife biologists. Cougars (*Puma concolor*), however, are a highly secretive species occurring at very low densities across the landscape, and thus their populations are difficult for biologists to accurately assess. The conventional, and most trusted, method entails physically trapping and radio-collaring as many cougars as possible in a population, and then performing a simple count to determine a minimum population size. While accurate, this method is prohibitively expensive, logistically challenging, and behaviorally disruptive to the study animal. Many noninvasive surveying techniques, such as camera trapping, have been proposed as alternatives for cougar populations, with the goal of providing accurate estimates of population size at a lower cost and with less impact on the study animal. These methods use detections of individual cougars in a mark-recapture framework, as opposed to a simple count, and have the benefit of being true, statistically rigorous estimates with confidence intervals. However, little research has been done to empirically verify the accuracy of these methods, or to determine their comparative cost-effectiveness. We compared the accuracy and cost-effectiveness of three types of noninvasive surveys applied on a

population of cougars in Northwest Wyoming. Between 2011 and 2014, we applied two surveys each of remote camera trapping, winter snow tracking, and scat detection dogs. To evaluate these methods, we estimated the density of the same cougar population using the conventional “capture-collar-count” method, and then used that estimate as a reference. Our research indicated that: 1) on a cost-per-detection basis, scat detection dog surveys were almost an order of magnitude less expensive the other methods; and 2) remote camera trapping may not be applicable to cougars due to the difficulty of distinguishing individual cougars in photographs. Our research should be valuable to research biologists, wildlife managers, or conservation entities responsible for monitoring cougar populations.

## ACKNOWLEDGMENTS

I would like to thank my advisor, Dr. Eric Gese, for his support, editorial skill, and patience during this project. He was always available to give sound advice, or a place to crash when needed. I would also like to thank my committee members, Dr. Dan Thompson of the Wyoming Game and Fish Department and Dr. Dan MacNulty for their thoughtful and valuable input. Additional thanks to Dr. Thompson, as well as Dr. Howard Quigley, without whom this project would not have been initiated; I would also like to sincerely thank them for trusting me with this project. Thank you to Dr. Mark Elbroch and the Teton Cougar Project team for their collaboration with captures, fieldwork, use of trucks and equipment, and for their vital support in general. Thanks to Boone Smith and the Smith family (as well as Lefty, Poncho, Trailer and Sue) for their expertise and endless energy during captures. I would especially like to thank Derek Craighead and Craighead Beringia South for supporting me throughout this project, especially during this final slog.

Thank you to Panthera, the Summerlee Foundation, the Paisley Foundation, and all the individual donors who made this project and the Teton Cougar Project possible. I would also like to thank the Wyoming Game and Fish Department, Grand Teton National Park, Bridger-Teton National Forest, and The National Elk Refuge for their support and collaboration. I also thank the Gros Ventre and Buffalo Valley Landowners for their cooperation.

Thanks to Ross Crandle for patiently entertaining my ill-conceived modeling and stats questions. Thanks to Jesse Newby for his valuable insight during the beginning stages of this research. Thanks to Marilyn Cuthill, Greg Davidson, Dr. Mark Elbroch, Dr.



Eric Gese, Patrick Lendrum, Dr. Kerry Murphy, Jesse Newby, Connor O'Malley, and Dr. Dan Thompson for participating in the cougar photo matching study (or for at least making a valiant attempt to get my lousy software to work). Thanks to Dr. Anthony Caragiulo of the American Museum of Natural History, and Dr. Lisette Waits and Dr. Jennifer Adams at the University of Idaho for genetic analyses. This project was, to say the least, field intensive; it would not have been possible without the hard work and enthusiasm of everyone in the field, many of whom worked voluntarily: thanks to Peter Abdu, Sean Beckett, Carl Bowden, Mike Boyce, Alex Cooke, Zach Dautrich, Sam Dwinell, Sophie Ellis, Sarah Farnsworth, Jenny Fitzpatrick, Jake Kay, Anna Kulser, Annie Loosen, Jesse Newby, and Anya Tyson for their help with the camera surveys and the winter tracking. Thank you to Greg Davidson (and Chevy and Moose) from Find It Detection Dogs for his hard work and expertise.

Finally, I thank my family for their support, my son Theo for giving me a new reason to smile, and, especially, my wife Charlotte for her encouragement and limitless patience.

Peter D. Alexander

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# CHAPTER 1

## INTRODUCTION

Several carnivore species have undergone dramatic contractions in their historic ranges due to habitat loss or habitat fragmentation (Laliberte and Ripple 2004), and there is a call for increased effort in carnivore conservation (Gittleman et al. 2001). Both the implementation and evaluation of any conservation efforts require accurate data on presence, abundance, and population trends. However, carnivores are generally wide-ranging and secretive, and their population statuses are often difficult to assess (MacKay et al. 2008). Cougars (*Puma concolor*) are no exception: large home ranges, low densities, and a highly cryptic nature make them an especially challenging species to monitor (Beier and Cunningham 1996, Logan and Sweanor 2001, Choate et al. 2006). Conventional methods for monitoring cougar populations involve capture, tagging, and radio-collaring, followed by radio-tracking. Location data can then be used in various approaches, ranging from simple enumeration (Cougar Management Guidelines Working Group 2005) to more complex home range analyses used to estimate density (McLellan 1989, Cooley et al. 2009). These capture-based estimates are considered the “gold standard” method for accurately determining cougar abundance or density (Cougar Management Guidelines Working Group 2005). However, they are time-consuming, prohibitively expensive, and logistically challenging. Furthermore, these methods require physical capture and handling (sometimes entailing an exhaustive pursuit with trailing hounds), which can be behaviorally disruptive and potentially hazardous to the study animal. Many state wildlife management agencies instead monitor cougar populations



with a low-cost framework that uses data from hunter harvests, known mortalities, and depredation events in conjunction with empirical knowledge specific to the area of interest. Although these harvest indices may provide valuable insight into general cougar population trends, they are affected by hunting effort and reporting rates, and do not provide a true population estimate (Beier and Cunningham 1996, Anderson and Lindzey 2005, Wolfe et al. 2015).

Noninvasive surveys may offer an accurate, low-cost alternative to the conventional methods outlined above. Data such as photographs from remote camera traps or DNA extracted from cougar scat may 1) be collected relatively cheaply and without directly interfering with the behavior of the study animal, and 2) provide the information needed for an accurate population estimate using a capture-mark-recapture (CMR) framework. Cougars, like many carnivores, may be ideal for noninvasive techniques due to traits such as territorial marking behaviors, inclination to respond to baited detectors due to curiosity, and unique track morphologies (Mackay et al. 2008). While noninvasive population monitoring techniques have been applied to cougar populations, there have not been any comprehensive studies in the past decade that have attempted to assess and compare the efficacy of several methods a single population. The goal of this project was to evaluate and compare the accuracy and financial feasibility of several noninvasive cougar population monitoring techniques. We evaluated the noninvasive methods using data from a long-term cougar ecology study conducted in the Southern Greater Yellowstone Ecosystem (the Teton Cougar Project); this study provided a radio-collared cougar population with a capture-based “gold standard” estimate of abundance. In the second chapter, we examine the “gold standard”

methodology. We review the literature, and identify the various sources of bias and ambiguity in this method. We pay special attention to issues that can be problematic when comparing capture-based cougar density estimates to noninvasively conducted estimates. We then develop a novel method for estimating density from capture data, and present density estimates for three years across two neighboring areas of differing cougar density. In the third chapter, we review the various noninvasive survey methods that have been applied to cougar populations, their potential benefits and shortcomings, and the available analysis methods used to determine population density. We apply three types of noninvasive surveys to the radio-collared population: scat detection dog surveys (Beckmann 1997, Long et al. 2008), winter track transects (Sawaya et al. 2011), and remote camera surveys (Kelly et al. 2008, Negrões et al. 2010). We use multiple analyses for each type of survey to estimate cougar density in the same two areas for which we calculated capture-based density. We then perform a cost-analysis of the three methods. In the fourth chapter, we summarize our research and draw conclusions, focusing on management implications.

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## **CHAPTER 2**

### **AN ANALYSIS OF INVASIVE TECHNIQUES USED TO DETERMINE POPULATION DENSITY OF COUGARS**

#### **ABSTRACT**

Determining population size and density of large carnivores is needed for informed decision-making by many conservation groups and wildlife management agencies. Many large carnivores, including cougars (*Puma concolor*), are cryptic, occur at low density, utilize large territories, and often occupy habitat characterized by dense cover and rugged terrain, making estimates of population size a logistical and economic challenge. Consequently, in most studies in North and South America, estimates of cougar population density often do not use conventional, statistically-based population estimation techniques, but instead employ direct census methods using physical capture, radio-tracking, and, essentially, enumeration of known individuals in a defined area. In this paper, we examined the sources of bias and uncertainty associated with various telemetry-derived techniques for enumerating the number of cougars in a defined area. Using various methods to address these issues, we estimated the density of a population of cougars in northwest Wyoming. Our methods included the incorporation of remote camera data, and a novel method for delineating the spatial denominator used in the density calculation. We GPS tracked 13 adult cougars (males = 5, females = 8) over 3 annual periods (Sep 2010 – Sep 2013). We delineated two effective trapping areas within the study area to use for the spatial component of the density calculations. We used proportional home range overlap to determine the abundance within the effective

trapping areas. The average cougar densities for the two areas, and the combined area, were 0.27, 1.07, 0.82 cougars/100 km<sup>2</sup>, respectively. Of note, the remote cameras detected uncollared cougars that would have been otherwise unaccounted for. Inclusion of these detections reduced the accuracy of our density estimates by an average of 15.3%, and highlighted the potential shortcomings of purported “saturation” trapping. Our method for delineating the area of density was particularly applicable to a study area with spatially varying cougar density that included areas of relatively low density, underscoring the importance of thoughtful design when estimating animal population density. This is especially relevant to large carnivore management, given current issues of range contraction and expansion.

## INTRODUCTION

Many carnivore species have undergone dramatic contractions in their historic ranges due to habitat loss or fragmentation, and direct human persecution (Laliberte and Ripple 2004), resulting in a greater need for expanded efforts in carnivore conservation (Gittleman et al. 2001). In recent decades, however, some carnivores have recovered at local range levels; examples of such recolonizations include some populations of grizzly bears *Ursus arctos* (Pyare et al. 2004) and cougars *Puma concolor* (Thompson and Jenks 2010). Reliable abundance estimates of large carnivores are necessary for identifying areas of extirpation or recolonization, and vital for the implementation and evaluation of conservation and management efforts. However, estimating abundance of carnivores is often hampered by issues that may be less common with other animal taxa (Boitani and Powell 2012). For example, cougars, as with many other large carnivores, are a cryptic,

sparsely occurring species utilizing large territories often characterized by dense cover and rugged terrain (Pierce and Bleich 2003), and thus do not lend themselves to conventional wildlife population estimation techniques such as point counts or aerial surveys. Classic capture-mark-recapture methods (CMR) or the Lincoln-Peterson Method (Seber 1982), are not necessarily appropriate, since these models require several assumptions that are rarely met in a cougar population. For example, cougars exhibit year-round potential for breeding and dispersal, thus violating the assumption of population closure. Capture probability likely varies between individual cougars and between subsequent captures of the same cougar, violating the assumption of equal catchability (Logan and Sweanor 2001, Amstrup et al. 2005). More sophisticated CMR models relaxing assumptions for population closure (Jolly 1965, Seber 1965) may be inappropriate given the assumptions that are violated due to the extended time period required for trapping and tagging cougars. Although recent developments in CMR models and novel methods of detection (such as genetic sampling or camera trapping) may resolve these issues, the most widely accepted method for estimating cougar population size remains direct counts of known individuals (Cougar Management Guidelines Working Group 2005). Indeed, the accepted “gold standard” method for estimating cougar density is derived from long-term radio-telemetry studies that attempt to radio-collar all or most resident cougars, followed by monitoring of individuals (Cougar Management Guidelines Working Group 2005). These types of studies allow researchers to identify residents versus transients, monitor births, deaths, immigrations and emigrations, and produce an informed enumeration of known resident cougars in a given area (e.g., Seidensticker and Hornocker 1973, Ross and Jalkotzy 1992, Spreadbury



et al. 1996). Despite the straightforwardness of this method, there are issues related to capture effort, spatial scale and certain subjective assumptions that researchers must decide (e.g., assigning demographic class). In this paper, we outline the various telemetry-derived census methods used in the published literature, including techniques used to reduce bias and subjectivity. One important caveat is that almost all published density estimates for cougars were calculated for the purposes of multi-seasonal demographic analysis within a single study area, and, as most studies acknowledge, are not especially useful for direct comparisons with other studies' population estimates or other population estimation methods. After outlining the various advantages and disadvantages of the different methodologies, we present a method by which we seek to minimize the identified biases and uncertainties. Although our methodology would not necessarily aid in direct comparisons with other studies' density estimates, our goal was to allow for comparisons with results from statistically-based noninvasive population estimators surveying the same study area.

### **Calculating Density**

Often cougar population estimates, especially from earlier cougar studies, are simple densities calculated by dividing the count of known marked resident cougars,  $N$ , by the study area size,  $A$  (e.g., Seidensticker and Hornocker 1973, Ross and Jalkotzy 1992, Spreadbury et al. 1996, Choate et al. 2006). While these measures of density appear to be inherently simple, the two variables in this ratio can nonetheless be difficult to precisely define and are susceptible to different biases related to capture effort, spatial extent, and natural spatial and temporal variation of cougar densities across a landscape. In the case of the numerator  $N$ , few cougar studies can confidently report to have

captured and counted all resident cougars in an area, and the raw count of marked cougars is generally considered a minimum known estimate or an underestimate (e.g., Neal et al. 1987, Franklin et al. 1999, Logan and Sweanor 2001, Choate et al. 2006). The denominator,  $A$ , can also be difficult to define objectively, and is prone to biases due to spatial inconsistencies and extrapolation issues (Smallwood 1997, Rinehart et al. 2014). Hereafter we refer to the spatial area used in calculating density as the “area divisor”, so as to avoid confusion in cases when it is not identical to the size of the study area.

### **Demographic Class**

Depending on study scope, independent subadult cougars or dependent juveniles (i.e., kittens) may or may not be included in population estimates. Choate et al. (2006) included subadults in their estimate, under the assumption these individuals were potentially available for hunter harvest. This is empirically true in some areas; in Wyoming, for example, 49% of cougar harvest across the state (2010-2012) was classified as subadult (Thompson 2013). Furthermore, subadults play an ecological role equal or similar to resident adults (Knopff et al. 2010), and inclusion of subadults in population estimates may be incorporated into management objectives. However, uncertainty of residency status, such as in instances when individuals are detected but not captured (and subsequently marked and tracked) may introduce problems (see below). Studies may not have the capacity for, or interest in, marking and monitoring cougar kittens. Maternal status of individual females in a population has important ecological implications by influencing kill rate (Knopff et al. 2010) and population growth. However, kitten survival rates are often low (Quigley and Hornocker 2010), and unless

kittens are rigorously monitored until they reach subadult or adult status, kitten counts may not necessarily contribute to a useful population estimate.

### **Unmonitored Individuals**

Even rigorous detection and capture efforts are unlikely to radio-collar all cougars within a study area. Often, but not necessarily, this shortcoming is confirmed by detecting, but failing to capture, unmarked cougars within the study area. These unmonitored individuals could either be residents that were missed in capture efforts, or transients moving through a study area. The difficulty thus arises on whether to incorporate these detections into a population estimate despite the potential for misattributing residency status or misidentifying an individual, thus resulting in double-counting single individuals or under-counting multiple individuals. Hereafter, “unmonitored residents” will refer to these detected, but uncollared and untracked, cougars.

Detections of unmonitored residents can be collected from multiple sources, such as mortalities from vehicle collisions or hunter harvest, track/spoor data, remote cameras, or other noninvasively collected data (e.g. Choate et al. 2006, Kelly et al. 2008, Sawaya et al. 2011). At a minimum, collecting these various types of detections is useful for researchers’ assessment of occupancy, movement patterns, and general insights into the population. However, the inability to reconcile different detection types (e.g., comparing a genetic sample and a camera-trap photograph) may result in a dataset that is less than the sum of its parts, and researchers may be limited in their use of these data.

Reported mortalities are useful as there is no risk of double counting a single individual, although transient status cannot necessarily be verified. In order to prevent

double counting, some studies (e.g., Robinson et al. 2008; Cooley et al. 2009*a, b*) limited inclusion of unmonitored residents strictly to reported mortalities. Other studies have accepted more ambiguous detections such as snow track detections: Choate et al. (2006), for example, assumed that same-sexed tracks repeatedly encountered in a watershed were from a single resident individual. While accurately attributing tracks to individuals is possible with rigorous field techniques and discriminant analysis (Lewison et al. 2001), we found no studies that used these methods and the accuracy of such data remains uncertain. This issue may be exacerbated in certain study areas where relatively localized “hot spots” of cougar presence occur, and detections of multiple individuals of the same sex or age is highly probable.

Finally, unmonitored residents (as well as completely undetected resident cougars) that are missed by initial capture efforts are sometimes “backlogged” if captured in subsequent seasons. Once a cougar was captured and the sex and age was determined, the previous enumerations would be adjusted under the assumption that a male likely immigrated at a certain age (usually 21 months) and a female cougar was likely a native to the area (Neal et al. 1987, Logan and Sweanor 2001, Choate et al. 2006, Cooley et al. 2009*a*).

Inclusion of unmonitored individuals in a census creates potential for errors and the possibility of generating a minimum density estimate that is greater than the true density. Despite being prone to error, inclusion of these data sources may nonetheless be preferable to the alternative of simply ignoring these individuals, as long as the issues outlined above are carefully considered.

### **Proportional Residency**

One technique used for animals with large home ranges is to calculate the proportional residency within the boundary of a defined area (i.e., the area divisor), with the intent of reducing biases associated with large, unevenly monitored populations and increase the precision of the population estimate. This has been done with other large carnivores such as grizzly bears (e.g. McLellan 1989) and leopards (*Panthera pardus*) (e.g. Balme et al. 2009), as well as cougars (e.g. Neal et al. 1987; Hopkins and Barrett 1991; Cooley et al. 2009*a, b*; Elbroch and Wittmer 2012; Allen 2014). Under this method, radio-collared animals contribute the proportion of their home range falling within the area divisor to the total count. For example, an animal with 45% of its home range overlapping the area divisor would contribute 0.45 individuals to the total count, and only animals with their entire home range contained within the area would count as a “whole” animal (Fig. 2.1). One benefit of this method is that it allows for the inclusion of individuals with home ranges extending beyond the study area or into areas with less frequent monitoring, without making any assumptions about the population density in those distal areas. Generally, this method assumes that all individuals occurring within the area divisor are captured. If unmonitored cougars in the area divisor are detected and assumed to be resident, researchers must either ignore this information or assign an unmeasured proportional residency. Cooley et al. (2009*b*) assigned the mean proportional residency of all radio-collared cougars to these unmonitored individuals.

In recent decades, home range analysis has improved markedly in precision and sophistication (Cagnacci et al. 2010, Kie et al. 2010). With modern GPS collars, the underlying location data for home range delineation has increased in accuracy and

collection rate. Besides allowing for a greater number of more accurate relocations, GPS collars can reduce bias in home range estimates for wide-ranging animals such as cougars (Kie et al. 2010). For example, older studies that triangulated VHF locations from the ground may have overestimated home range sizes for animals distal from human access points due to telemetry error (Withey et al. 2001). This bias in home range shape would potentially translate to a biased measure of proportional residency, depending on the location of VHF triangulation points in relation to the area divisor. Improved location data have in turn improved the precision of home range delineation with more sophisticated home range estimators such as kernel density estimation (KDE; Worton 1989) or Brownian Bridge movement models (BBMM; Bullard 1991). Ostensibly, measures of proportional residency would not be greatly affected by the precision of a home range estimator, since the proportionality of spatial overlap on the area divisor should remain constant between different home range estimators (provided that relocation data are spatially unbiased). However, the modern estimators listed above are likely more appropriate than traditional minimum convex polygons, since they tend to better exclude space unused by animals and reduce the potential for mis-delineating a home range inside or outside the area divisor (Walter et al. 2009). See Figure 2.2 for a comparison of various home range delineations and corresponding proportional overlap values for a hypothetical area divisor.

### **Delineating the Area Divisor**

Objectively delineating the spatial area over which animal density is calculated can be complicated by several factors. The predefined study area can be used to determine the area divisor, but a study area is often defined wholly or partially by

political boundaries or other subjectively defined boundaries, and may not be biologically appropriate to the study animal or well-suited to animal detection and capture efforts. Except in rare cases such as “island” populations of cougars (e.g., Logan and Sweanor 2001, Bacon 2010), most cougar study areas only encompass a fragment of the spatial extent of the population being studied. Calculating the proportional residency may help reduce bias related to uneven monitoring across expansive home ranges, but may not address issues related to extrapolating density estimates across the greater landscape. For example, researchers may “go for the low hanging fruit” by focusing detection and capture efforts in areas with high quality cougar habitat relative to the surrounding landscape. Consequently, in extrapolating the estimated density to the larger landscape, there is a potential for overestimating density (i.e., sampling frame error; Smallwood and Schonewald 1996, Rinehart et al. 2014). Conversely, if areas with low detection effort are included in the area divisor, there is the potential to underestimate density due to the failure to detect resident cougars.

There are two techniques commonly cited by cougar studies for delineating the area divisor beyond simply using the predefined study area. One method reduces capture effort bias through the use of a “trapping area” (McLellan 1989). McLellan (1989) estimated grizzly bear density using proportional residency within an area defined by the trapping effort (i.e., where the majority of trapping sites were located), as opposed to the extent of the entire study area. A second technique attempts to reduce the subjectivity of delineating the area divisor by defining boundaries *a posteriori* around aggregate cougar locations. For example, Hopkins and Barrett (1991) proposed an area divisor based on an average of a weekly minimum convex polygon enclosing all radio-collared cougars’

locations. More recently, studies have used a composite of cougar home ranges (defined by KDEs) to delineate the area (e.g., Cooley et al. 2009*a, b*; Elbroch and Wittmer 2012). These latter methods could be described as “letting the study animal decide”, which presumably reduces the bias from subjectively defining the area divisor boundaries. However, unless detection and trapping efforts are equivalent across the aggregate home ranges, there is the probability of telemetered cougar home ranges extending into areas that were not as thoroughly trapped, and where there is a greater chance of undetected cougars occurring (Fig. 2.3). Elbroch and Wittmer (2012) essentially combined the two techniques by first identifying an area where they believed they had captured all resident cougars (analogous to a trapping area), then aggregated the cougar KDE home ranges that fell completely within that area. While this method may reduce bias associated with uneven detection and capture effort, telemetered cougar home ranges, as a matter of course, would exclude areas where cougars were not detected despite equal effort (Fig. 2.3). Limiting the density estimate exclusively to areas occupied by the study animal may not generate a realistic pattern of abundance in the study area as a whole (Smallwood 1999). For example, certain parts of a study area may have lower cougar abundance despite apparent habitat quality. This could be due to factors such as differing hunting pressure, human disturbance, prey abundance, or interspecific competition with other large carnivores such as wolves (Kortello et al. 2007, Bartnick et al. 2013, Lendrum et al. 2014).



## STUDY AREA

The greater study area encompassed 5,120 km<sup>2</sup>, including much of the Jackson Hole basin and adjacent lands in northwest Wyoming. The area was delineated by the Teton Range in Grand Teton National Park (GTNP) on the west, the Gros Ventre Range on the east, the Teton Wilderness Area on the north, and on the south by Wyoming state highway 22 and the Cache Creek drainage. Most lands within the study area were administered by the U.S. Forest Service (Bridger-Teton National Forest), the National Park Service (Grand Teton National Park), and U. S. Fish and Wildlife Service (National Elk Refuge). A small percentage (~ 5%) was comprised of privately owned ranches or residential areas (Fig. 2.4). Elevations in the study area ranged from ~1,800 m in the Jackson Hole basin to >3,600 m in the mountains. The area was characterized by short, cool summers and long winters with frequent snowstorms. Average monthly temperature minimums and maximums ranged from -17.3°C and -3.4°C in January, to 5.3°C and 26.9°C in July. Precipitation occurred mostly as snow, and mean maximum snow depths ranged from 100 cm at lower elevations to >245 cm at intermediate elevations of 2,000 – 2,400 m (Grand Teton National Park 2015).

Plant communities included cottonwood (*Populus angustifolia*) riparian zones interspersed by sagebrush (*Artemisia spp.*) uplands at lower elevations. At intermediate elevations, aspen (*P. tremuloides*), Douglas-fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*) were the dominant species. Spruce (*Picea engelmannii*) and fir (*Abies lasiocarpa*) were the primary tree species at the higher elevations (Marston and Anderson 1991, Knight 1996).

Primary prey species available included mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), white-tailed deer (*O. virginianus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and various small to medium sized mammal and avian species. The study area also included all historically occurring large carnivores: grizzly bears (*Ursus arctos*), black bears (*U. americanus*), and gray wolves (*Canis lupus*), as well as several mesocarnivores, including coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*), and possibly two other sympatric felids: bobcats (*Lynx rufus*) and lynx (*Lynx canadensis*).

## METHODS

### Cougar Capture and Radio-collaring

Cougar capture efforts were focused in two areas within the greater study area: the Gros Ventre River and Buffalo Valley drainages (Fig. 2.5); capture efforts in these areas were used to define the area divisors in order to improve the precision of our density estimates, as described above. We captured and radio-collared cougars primarily during winter months (November to April) when snow cover facilitated tracking and enabled researchers to identify cougar presence. Density estimates were derived from radio-collars deployed between 2010 and 2014, although some additional analysis utilized telemetry data from as early as 2004. After snowfall events, predetermined transects were surveyed on foot, truck or snowmobile to search for cougar tracks. Transects were selected based on topographic features characteristic of cougar habitat or travel routes, and ease of access for trackers. Once we located tracks and determined them to be from an unknown adult cougar without very young kittens ( $\leq 4$  months old), we typically used trailing hounds to pursue the cougar into a tree or rocky outcrops where

we could safely approach and immobilize the cougar following procedures outlined by Sikes and Gannon (2011), Quigley (2000), and the Jackson Institutional Animal Care and Use Committee (Protocol 027-10EGDBS-060210). Occasionally circumstances allowed for a walk-in type of cage trap to be used (Tru-Catch Traps, Belle Fourche, South Dakota, USA), wherein bait such as road-killed deer was used to lure the cougar. We initially administered ketamine at 4.0 mg/kg, followed by medetomidine at 0.07 mg/kg. In the case of “treed” cougars, we initially administered the ketamine dose via a CO<sub>2</sub> powered dart-gun (Dan Inject North America, Fort Collins, Colorado, USA). We then climbed the tree and used rope to hobble and lower the semi-immobilized cougar to the ground, where upon the medetomidine dose was hand-injected. Once fully immobilized, the cougar’s heart rate, temperature, and respiratory rate were monitored every 5 minutes. We collected genetic samples (hair and tissue), body measurements, and estimated age using tooth condition (Heffelfinger 2010) and a gum line recession metric (Laundre et al. 2000). We fitted cougars with GPS collars (Lotek, Newmarket, Ontario, Canada; Northstar, King George, Virginia, USA; Televilt, Bandygatan, Sweden; Telonics, Mesa, Arizona, USA; Vectronics, Berlin, Germany), programmed to collect locations between 4 and 10 times per day. After animal processing was completed, and sufficient time had elapsed to allow for the metabolism of the ketamine (~60 minutes), we administered Atipamezole at 0.375 mg/kg to reverse the effects of the medetomidine. We monitored cougars during recovery until they were able to safely depart the area on their own, typically 5 – 15 minutes after the reversal drug was administered.

## Density Estimate

We used GPS collar data and proportional residency to estimate the minimum density of cougars in the area divisor as defined by trapping efforts (McLellan 1989), and amended that minimum density with other sources of cougar detections, including remote camera detections from a static camera trapping array and remote video detections from cameras placed at cougar prey-sites. Although data was available for dependent kittens, we limited our enumeration to independent, non-transient adults and subadults, as this was more comparable to other density estimates. We chose to use proportional residency in an area divisor defined by trapping effort in order to reduce bias created by uneven capture effort across the greater study area. We did not delineate sampling area with aggregate home ranges (Cooley et al. 2009*a, b*), as we believed the areas of trapping effort better represented the study area as a whole, including areas of apparently suitable cougar habitat that had low or zero cougar density, based on the very low detection rates of cougars during capture efforts, remote camera surveys, and scat detection dog surveys (Chapter 3).

We delineated the area divisor based on where the majority of detection and capture effort occurred, with the exception of replacing radio-collars or opportunistic captures that occasionally occurred outside of this area. We based this boundary around the winter transects used by capture teams, and which were rarely or never crossed by unknown cougars by the conclusion of a capture season. While McLellan (1989) used a minimum convex polygon around point locations of bear trapping stations, our “trapping stations” were defined by the 2-dimensional snow transects. To represent the effective trapping area of the transects, we buffered the transects by the average female home

range radius (analogous to the commonly used mean-maximum-distance-moved metric) during winter trapping months, calculated from all GPS collar data spanning the history of the study (Fig.2.2). Home ranges were defined by 95% KDE using the plug-in bandwidth (see below). We defined the resulting polygon as a space in which any or almost any resident cougar would be detected, captured, and radio-collared. This method allowed for a more systematic area divisor than the composite home range method (e.g., Cooley et al. 2009*a, b*; Elbroch and Wittmer 2012; Allen et al. 2015), which gave a less biased density estimate across the whole study area (including areas with very low density); this method also allowed for the comparison of results from alternative density estimators with spatially corresponding extents (i.e., noninvasive sampling and population estimators; Chapter 3).

Cougar densities were calculated separately and together for the Buffalo Valley and the Gros Ventre drainages, for the years 2011 through 2013 (years were defined as September 1 to August 30<sup>th</sup> of the following year). All spatial analysis was done in R (R Version 3.0, [www.r-project.org](http://www.r-project.org), accessed 10 Oct 2013) and Geospatial Modeling Environment (Geospatial Modeling Environment Version 0.7.2.0, <http://www.spatialecology.com/gme>, accessed 31 Aug 2012), with visualization of processes implemented in ArcMap 10.2 (Environmental Systems Resource Institute 2013). We delineated home ranges in R with 95% KDEs using the plug-in method for bandwidth selection (Jones et al. 1996). This was performed using the *adehabitat* package (Calenge 2011) and the *ks* package (Duong 2014), as outlined by Walter and Fischer (2015). We also used the R packages *maptools* (Bivand and Lewin-Koh 2014), *rgeos* (Bivand and Rundel 2011), and *shapefiles* (Stabler 2014) to build trapping buffers and

calculate proportional overlap of the resulting polygons. Densities were scaled to cougars/100 km<sup>2</sup>.

*Appropriateness of trapping buffer.*— One critical assumption behind our selection of the winter trapping buffer as the area divisor was that most or all cougars that used the space within the buffer could be detected and captured from the winter trapping transects. However, a hypothetical cougar home range could have potentially overlapped the trapping buffer, while failing to intersect the transect line (thus preventing the cougar from being detected and captured), resulting in an underestimation of cougar density. We tested our assumption that the winter trapping transects were adequate in transecting the home ranges of cougars that were resident in the area divisor with a resource selection function (RSF; Manly et al. 2002). We constructed the RSF under a use-availability framework using the R package ResourceSelection (Lele et al. 2013) to compare available locations to radio-collared cougar winter locations within the winter trapping buffer. We note that these models were not intended to test any underlying ecological process, but only to test if there was evidence of cougars avoiding the designated transects.

### **Unmonitored Individuals**

We followed protocols by Neal et al. (1987), Logan and Sweanor (2001), Choate et al. (2006), and Cooley et al. (2009a) to incorporate detections of unmonitored cougars into the yearly enumerations when  $\geq 2$  detections could be confidently attributed to a single non-transient individual. These protocols also allowed for “backlogging” the enumerations in cases when individuals were captured in subsequent years and, depending on age and sex, were likely present in previous years. Detections were

primarily collected from remote cameras placed within or adjacent to the trapping area. Remote camera detections were collected from two sources: remote video cameras placed at cougar prey-sites, and remote camera stations setup with scent-lure. The video data was generated by a concurrent study within our study area examining cougar foraging behavior using remote video cameras (Bushnell Trophy Cam HD Max, Bushnell Outdoor Products, Overland Park, Kansas, USA) placed at cougar prey-sites identified by GPS clusters (Anderson and Lindzey 2003). GPS collar data was transmitted via satellite 2 to 6 times per day, allowing researchers to identify and visit prey-sites to install cameras. Generally this could be done within the first 48 hours after a kill, often before the cougar had consumed or abandoned a kill. The video data indicated that prey-sites were occasionally visited by cougars other than the individual from which the prey-site was detected, including uncollared individuals. Uncollared cougars were also detected by means of an array of 55 remote camera stations, split between the Gros Ventre and Buffalo Valley drainages. Stations were operational from June to September of 2012 and 2013. The majority of camera stations ( $n = 43$ ) used a non-reward scent lure comprised of aged cattle blood; the additional sites ( $n = 12$ ) used a cologne based “curiosity” lure and were placed along high-use trails where we were restricted from using the blood-based lure (see Chapter 3 for more information on the remote camera station study design). We identified and distinguished individual cougars in photographs and videos based on artificial tags, physical features (i.e., kinked tails, facial features, or size), and spatial/temporal distance between detections. Unmonitored cougars were only included in the enumeration when multiple detections could be confidently attributed to the same individual, indicating non-transient status. We also included detections from hunter

harvest and other known mortalities of unmonitored adult cougars. However, we note that hunting pressure was relatively low in the study area. The mean harvest rate for the 6,434 km<sup>2</sup> management area (Hunt Area 2) in which the study area was located was 2.0 cougars per year between 2009 and 2013 (Thompson 2010, 2013; Clapp 2014). Detections only included hunter harvest mortalities that occurred within the Buffalo Valley and Gros Ventre drainages, and did not include subadults since non-transient status could not be verified (except in cases when residency could be backed up by other sources of detection).

We backlogged newly radio-collared or detected cougars to previous seasons following protocols of Logan and Sweanor (2001), Robinson et al. (2008), and Cooley et al. (2009a), which assumed that males immigrated at 21 months and females were native to the study area. Proportional residency was unknown; we therefore assigned either the mean proportion of all radio-collared cougars of the same sex, or, if the cougar was captured in subsequent seasons, back-logged that individual's proportional residency or mean proportional residency (if tracked for multiple years).

*Percent accuracy.*— We estimated capture success using the percent accuracy metric developed by Logan and Sweanor (2001):

$$PA = [1 - BL_{year\ i} / (BL_{year\ i} + C_{year\ i})] \times 100$$

where BL is the number of backlogged individuals for year i, and C is the number actually tracked and enumerated. We also calculated a modified version of this equation that used the proportional residency values instead of the whole number enumerations used in the original equation.



## RESULTS

### Capture, Tracking and Home Range Delineation

We GPS tracked 13 individual adult cougars over the course of the study from September 2011 to August 2014. The trapping events in which these individuals were captured and radio-collared occurred between the winters of 2007 and 2014. Trapping effort (as expressed in km transected) was only quantified in 2012 and 2013; mean effort was 684.5 km ( $\pm 197.9$  SD,  $n = 2$ ). We note that all years were similar in capture effort, and used the same trapping transects (Table 2.1). The GPS tracked individuals included 5 males and 8 females; dependent kittens were also marked but not included in this analysis. Excluding recaptures or captures of juveniles that were aided by radio-telemetry, we performed 12 “blind captures” for 11 of the individuals which were initiated by track detection along the snow transects. All but one of these were detected on the trapping transects. The GPS location data was collected and divided into 3 annual time periods covering September 1 – August 30. We calculated annual home ranges for 7, 8, and 8 individual cougars for each year (2011-2013), respectively.

Mean annual home range size for male cougars (weighted by individual) ranged from 223.9 km<sup>2</sup> to 538.6 km<sup>2</sup> ( $n = 5$ ,  $\bar{x} = 369.43 \pm 134.9$  SD). Mean annual home range size for female cougars ranged from 67.3 km<sup>2</sup> to 219.4 km<sup>2</sup> ( $n = 8$ ,  $\bar{x} = 148.1 \pm 67.7$  SD). One newly independent female (F097) collected 19 locations in 2012, and was excluded for that year. One male (M029) was fitted with an advanced radio-collar which collected 6,270 locations in 2013. Excluding these outliers, quantity of yearly GPS relocations per individual ranged from 276 to 1,896 ( $\bar{x} = 894.5 \pm 445.0$  SD). One additional individual (M085) was captured in the subsequent 2014 season and was determined to have been a

resident cougar in previous seasons based on age and remote camera data. When accounting for backlogged home ranges, there were 11, 10, and 9 calculated individual home ranges included in each year (2011-2013), respectively.

### **Area Divisor Delineation**

To construct the area divisors, we first determined the average home range size during winter for females by examining all GPS-based winter home ranges collected as early as 2004. Home ranges were only included if the individual's seasonal home range was comprised of a minimum of 50 relocations, as recommended by Seaman et al. (1999), and incorporated a minimum of 100 days. The mean female home range size, weighted by individual, during winter capture seasons (defined as November 15 to April 15, based on average monthly snow coverage; Grand Teton National Park 2015) was  $102.4 \text{ km}^2$  ( $\pm 86.8 \text{ SD}$ ,  $n = 9$ ). The resulting geometric radius was 5.7 km, creating area divisors of  $843.7 \text{ km}^2$ ,  $783.1 \text{ km}^2$ , and  $1,570.3 \text{ km}^2$  for the Gros Ventre, Buffalo Valley, and combined areas, respectively. There was a 5.6% overlap between the two areas.

### **Unmonitored Cougars**

We enumerated an additional three unmonitored cougars into the density estimate. One female was captured but not tracked due to a failed radio-collar; this individual was first captured in early 2010 and visually sighted as late as early 2013. Using photo and video data from remote cameras, we identified a minimum of two additional unmonitored females that we determined to be adult residents. Outside of these unmonitored residents, the remote camera stations collected 17 and 20 detections of uncollared cougars in 2012 and 2013, respectively. These detections were either determined to be individuals which

were captured in subsequent years (and were accordingly backlogged), or could not be confidently identified as resident individuals. The three unmonitored residents were assigned the average proportional residency value for the sex and area divisor in which they were detected. From 2011 through 2014, the Wyoming Game and Fish Department reported 10 cougar mortalities in the local management area (Hunt Area 2) due to hunter harvest (Thompson 2013, Clapp 2014, Wyoming Game and Fish Department 2015). Seven harvests were reported outside of the watersheds in which the area divisor was drawn. The remaining three were radio-collared cougars that were already included in the enumeration.

### **Density Estimates**

The mean unadjusted density estimates covering all three years were 0.13, 0.85 and 0.50 cougars/100 km<sup>2</sup> for the Buffalo Valley, Gros Ventre, and combined areas, respectively. When adjusting for uncollared residents, the estimates averaged 0.27, 1.07, 0.82 cougars/100 km<sup>2</sup> (Table 2.2). To examine the sensitivity of density estimates to buffer size, we also calculated density estimates using area divisors based on one standard deviation above and below the mean female winter home range (Table 2.3).

*Percent Accuracy.*— We estimated capture success using Logan and Sweanor's (2001) percent accuracy method. Before accounting for unmonitored residents (and only using radio-collared individuals for backlogging), percent accuracy averaged 74.2% across the trapping areas and years. When including uncollared individuals detected from video detections, accuracy averaged 58.9%. Similar numbers are reported when using proportional residency, averaged with and without the inclusion of unmonitored individuals (Table 2.4).

*Appropriateness of trapping buffer.*— Radio-collared cougars selected for lower elevations within the trapping buffer ( $\beta = -2.979$ ,  $P < 0.001$ ). Transects were generally located along drainage bottoms and lower elevations, suggesting that cougars, if present within the trapping buffer, would not avoid the lower elevations and therefore should be detectible along transects. We ran a second RSPF using distance-to-transect as an attribute, and found that radio-collared cougars selected against areas distal to the winter transects themselves ( $\beta = -1.364$ ,  $P < 0.001$ ), suggesting that cougars present within the winter trapping buffer should be detected at the transect.

## DISCUSSION

Our density estimates for the Gros Ventre area were within the range of published estimates from other cougar studies in North America (Smallwood 1997, Quigley and Hornocker 2010). Our estimates for the Buffalo Valley area were below the lowest reported estimates that we found in the literature. The differences in density estimates between the Buffalo Valley and Gros Ventre areas were not especially surprising, given the former's lower capture success, as well as the lower detection rates from other noninvasive sources of detection (i.e., remote camera and scat detection dog surveys; Chapter 3). Possibly, the differences in densities were due to intra-guild competition with recently recolonized wolves (Bartnick et al. 2013, Lendrum et al. 2014, Elbroch et al. 2015) or grizzly bears in the Buffalo Valley area. However, given these carnivores' large home ranges, low densities, and cryptic natures, research on their interactions is notoriously difficult (Kortello et al. 2007), and conclusive interpretation may remain dubious.

Our criteria for including unmonitored residents in the enumeration was more conservative than those used by Choate et al. (2006) and Robinson et al. (2008). For example, we ignored several remote camera detections that could not be verified as resident cougars. This was in part due to the difficulty in identifying individual cougars (see Chapter 3), and it was highly possible that some of these detected individual cougars were indeed residents. Thus, our estimates were much more likely to have been underestimates than overestimates of the true density. Using the Logan and Sweeney (2001) method, our mean percent accuracy metric (before adjusting for unmonitored residents) was 74.2%. Logan and Sweeney (2001) reported an average percent accuracy of 87.4%, and Sawaya et al. (2011) reported an average of 90.5% accuracy. Critically, our average percent accuracy measure dropped 15.3% to 58.9% when including the unmonitored resident cougars detected by remote camera. This reduction in accuracy likely would not have been realized without the aid of remote cameras and remote video surveys, and highlights the difficulties and limitations of purported saturation trapping. While this thesis addresses certain biases in cougar trapping and telemetry-based density estimation, other biases in trapping effort and capture success likely remain, despite our methodology. Cougar trapping was a relatively protracted process with low capture rates. It was often dependent on several intangible and interactive factors including weather conditions, physical and political accessibility, and the experience and behavior of both researchers and trailing hounds. To some degree, it was an inherently opportunistic and haphazard process, and precisely quantifying effort was difficult. Nonetheless, we recommend careful recording of capture effort to minimize the uncertainties and subjectivity that could otherwise bias density estimates.

In this paper, we argue that an area divisor was best defined by the effective trapping area, as opposed to the composite home range method used by Robinson et al. (2008), Cooley et al. (2009*a, b*), Elbroch and Wittmer (2012), and Allen et al. (2015). Our method reduces bias by 1) preserving the sampling frame near the trapping effort, whereas a composite home range could include areas distal from the sampling effort, especially given the large home ranges of cougars, and 2) including sampled areas with low or no cougar density, which would otherwise be excluded by a composite home range. We note the studies by Elbroch and Wittmer (2012) and Allen et al. (2015) specifically addressed the issue of uneven sampling effort by restricting the composite home range to an area of high trapping effort. However, the area divisors used by Elbroch and Wittmer (2012) and Allen et al. (2015) were 450 km<sup>2</sup> and 402 km<sup>2</sup>, respectively. These spatial extents were on the lower range of Smallwood's (1997) review of published estimates of cougar density, which found a negative correlation between density estimates and study area (i.e., area divisor) size. Our combined area divisor was ~8% smaller than the mean size of 1,700 km<sup>2</sup> as reported by Smallwood (1997).

Furthermore, the composite home range method may be biased towards “hot spot” areas of cougar presence, and may not accurately reflect the natural variations in cougar density across a landscape. Indeed, Smallwood (1997) found that almost all published density estimates were likely focused at cougar aggregations (i.e., “hot spots”), and called for future studies to increase their spatial extent to areas beyond these aggregations. Our area divisors included such areas that had very low cougar density. Management or conservation efforts may choose to monitor such areas, especially when evaluating possible scenarios of recolonization or extirpation, and the methods used by the studies

listed above would not necessarily be appropriate. Furthermore, cougar populations at a regional scale likely exhibit spatially shifting aggregations over the course of several years (Smallwood 1997). As many carnivore populations are currently undergoing varying degrees of range contraction and expansion (Laliberte and Ripple 2004), regional population densities may be affected by poorly understood inter-specific interactions with other newly or formerly sympatric carnivore species (Kortello et al. 2007). Due to these issues, cougar density estimates that are spatially limited to high density areas (either due to purposely focusing research at population aggregations, or through the use of a composite home range based area divisor), may not be representative of the regional cougar population on a whole or its long-term trend. Researchers should carefully consider the spatial extent of detection or capture efforts and the potential biases related to variations in animal density across a landscape.

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Table 2.1. Winter snow transects for the detection and capture of cougars, listed by mode of transect and trapping area, northwest Wyoming, 2011-2013.

|                  | Distance (km) | % of total |
|------------------|---------------|------------|
| Mode of Transect |               |            |
| Foot             | 42.91         | 18.97%     |
| Snowmobile       | 136.77        | 60.48%     |
| Truck            | 46.46         | 20.55%     |
| Total            | 226.14        | 100.00%    |
| Trapping area    |               |            |
| Buffalo Valley   | 123.10        | 54.44%     |
| Gros Ventre      | 103.04        | 45.56%     |
| Total            | 226.14        | 100.00%    |

Table 2.2. Density estimates (cougars/100 km<sup>2</sup>) for a population of cougars in northwest Wyoming, 2011-2013, using enumeration and proportional residency.

|      |                | Enumeration | Adjusted enumeration | Density | Adjusted density |
|------|----------------|-------------|----------------------|---------|------------------|
| 2011 | Buffalo Valley | 1.60        | 2.72                 | 0.20    | 0.34             |
|      | Gros Ventre    | 7.91        | 9.77                 | 0.94    | 1.16             |
|      | Combined areas | 9.26        | 11.90                | 0.59    | 0.91             |
| 2012 | Buffalo Valley | 0.50        | 1.62                 | 0.06    | 0.20             |
|      | Gros Ventre    | 7.91        | 9.77                 | 0.94    | 1.16             |
|      | Combined areas | 8.22        | 10.86                | 0.52    | 0.84             |
| 2013 | Buffalo Valley | 0.90        | 2.02                 | 0.11    | 0.25             |
|      | Gros Ventre    | 5.68        | 7.55                 | 0.67    | 0.90             |
|      | Combined areas | 6.25        | 8.89                 | 0.40    | 0.72             |

Table 2.3. Enumerations and density estimates of cougars in Northwest Wyoming, using area divisors based on one standard deviation above and below the mean female home range size. Area divisors were drawn by buffering capture transects with the geometric radius of the mean female home range.

|      |                | Adjusted enumeration |                    | Adjusted density   |                    |
|------|----------------|----------------------|--------------------|--------------------|--------------------|
|      |                | buffer -1 $\sigma$   | buffer +1 $\sigma$ | buffer -1 $\sigma$ | buffer +1 $\sigma$ |
| 2011 | Buffalo Valley | 1.59                 | 3.13               | 0.40               | 0.30               |
|      | Gros Ventre    | 6.99                 | 10.68              | 1.80               | 0.94               |
|      | Combined areas | 8.47                 | 12.77              | 1.30               | 0.75               |
| 2012 | Buffalo Valley | 0.90                 | 1.97               | 0.22               | 0.19               |
|      | Gros Ventre    | 6.47                 | 10.71              | 1.67               | 0.95               |
|      | Combined areas | 7.26                 | 11.74              | 1.14               | 0.70               |
| 2013 | Buffalo Valley | 1.10                 | 2.41               | 0.27               | 0.23               |
|      | Gros Ventre    | 5.14                 | 8.34               | 1.33               | 0.74               |
|      | Combined areas | 6.13                 | 9.68               | 1.00               | 0.60               |

Table 2.4. Percent accuracy of density estimates of a cougar population in northwest Wyoming, 2011-2013 using the method described by Logan and Sweanor (2001), as well as a modified method using proportional residency. The “adjusted” values include residents that were detected, but not radio-collared and tracked.

|                               | Percent accuracy | Adjusted percent accuracy | Difference |
|-------------------------------|------------------|---------------------------|------------|
| Logan-Sweanor method          |                  |                           |            |
| 2011                          | 63.6%            | 50.0%                     | 13.6%      |
| 2012                          | 70.0%            | 53.8%                     | 16.2%      |
| 2013                          | 88.9%            | 72.7%                     | 16.2%      |
| Proportional residency method |                  |                           |            |
| 2011                          | 69.5%            | 54.1%                     | 15.4%      |
| 2012                          | 77.8%            | 58.9%                     | 18.9%      |
| 2013                          | 89.9%            | 70.2%                     | 19.7%      |

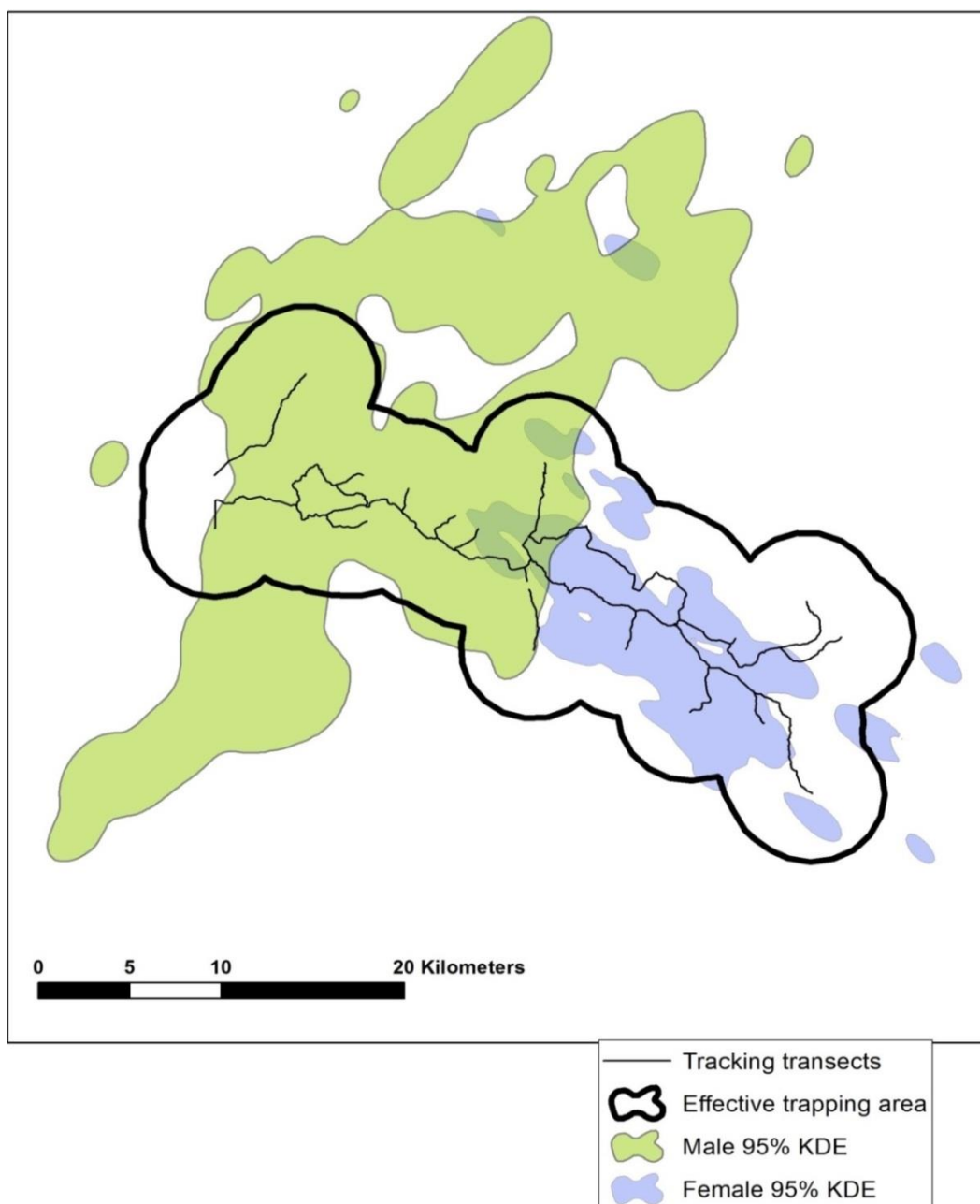


Figure 2.1. Example of population density estimation using enumeration of proportional residency. This example represents 39% of a male home range (green), and 91% of a female home range (blue) intersecting an effective trapping area. In this scenario, the total density would be 1.3 animals in the trapping area.

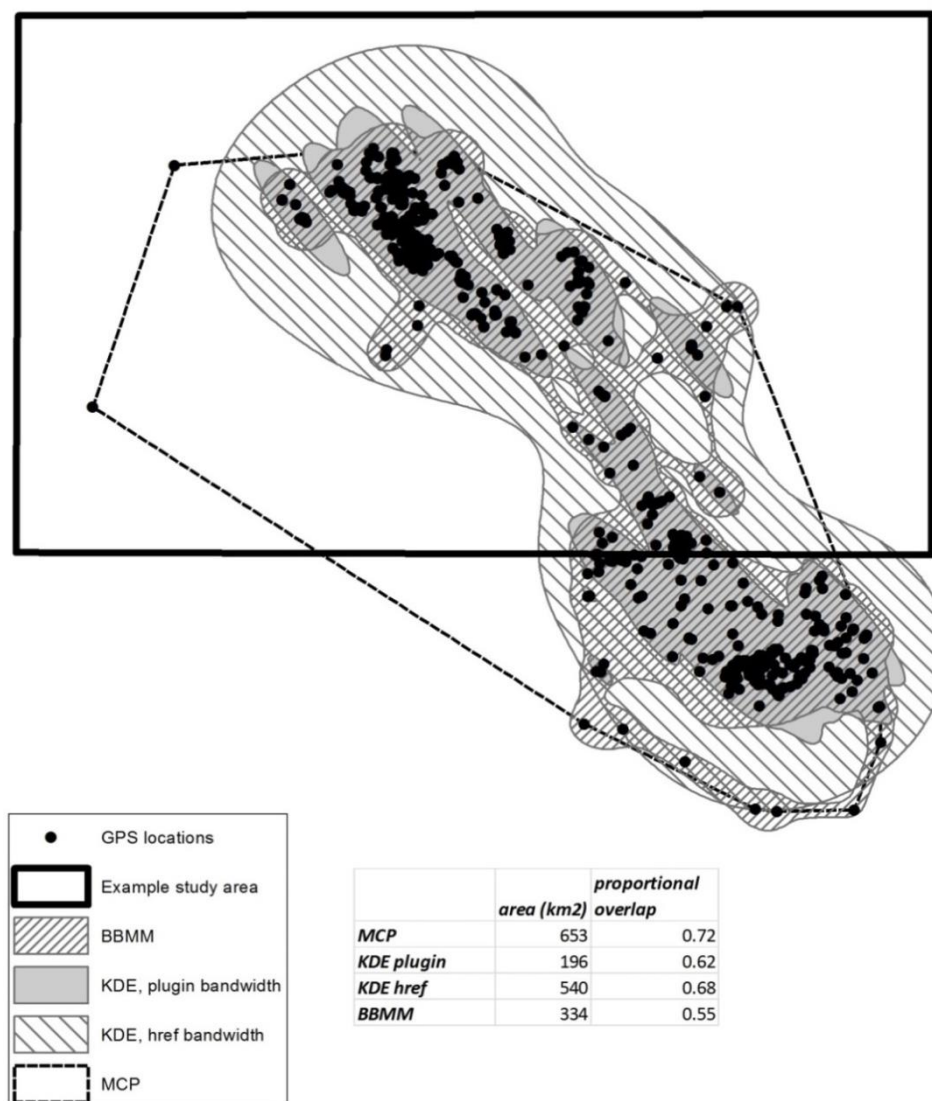


Figure 2.2. Several home range delineations using location data from one female cougar, including Brownian Bridge Movement Model (BBMM), minimum convex polygon (MCP), and Kernel Density Estimation (KDE) using both “plugin” and “href” bandwidths. Home range delineations are overlaid on a hypothetical study area in which proportional residency values are calculated.

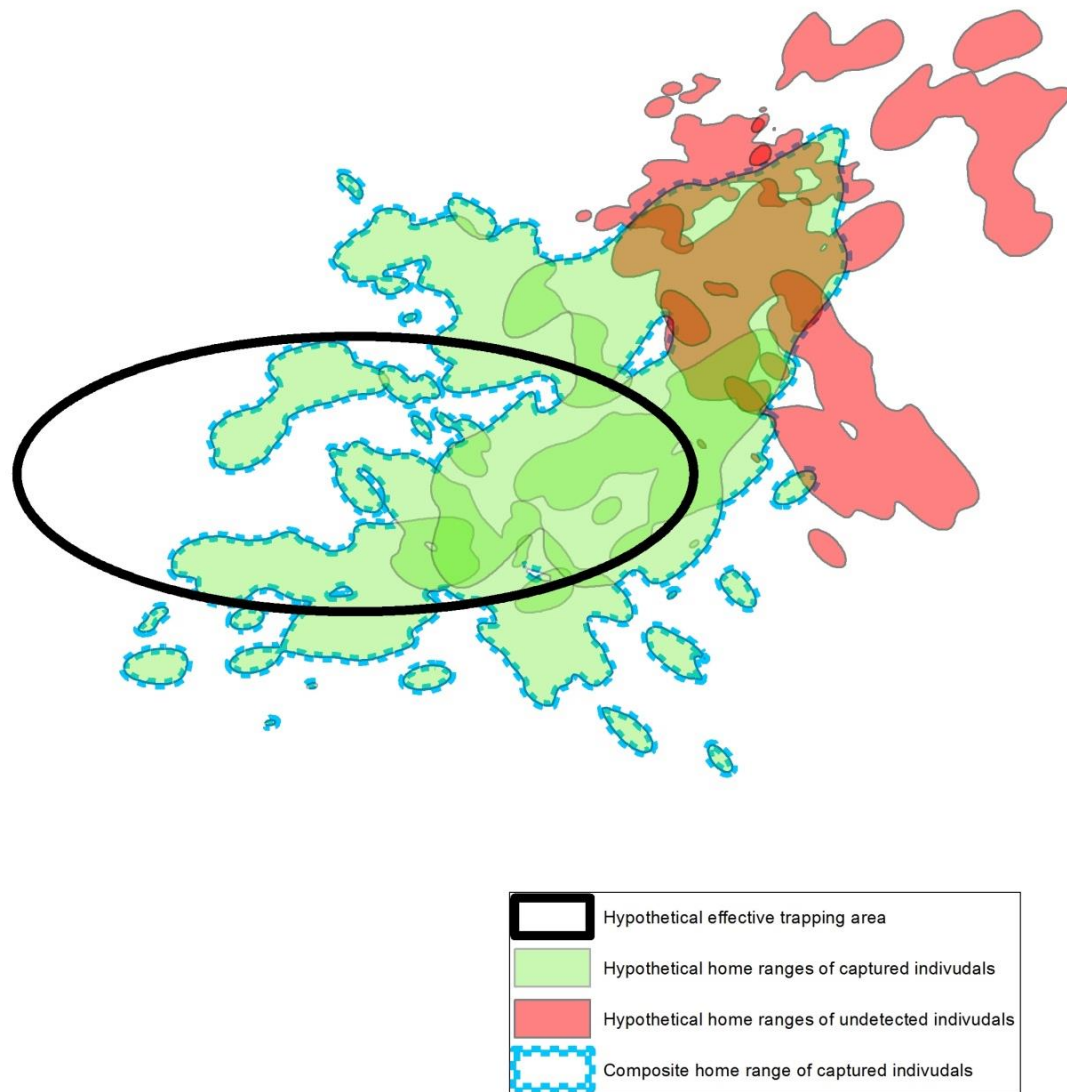


Figure 2.3. Hypothetical home ranges of telemetered cougars (green) and undetected cougars (red), demonstrating the potential to underestimate density when using a composite of telemetered home ranges as the area over which to calculate proportional residency and density.

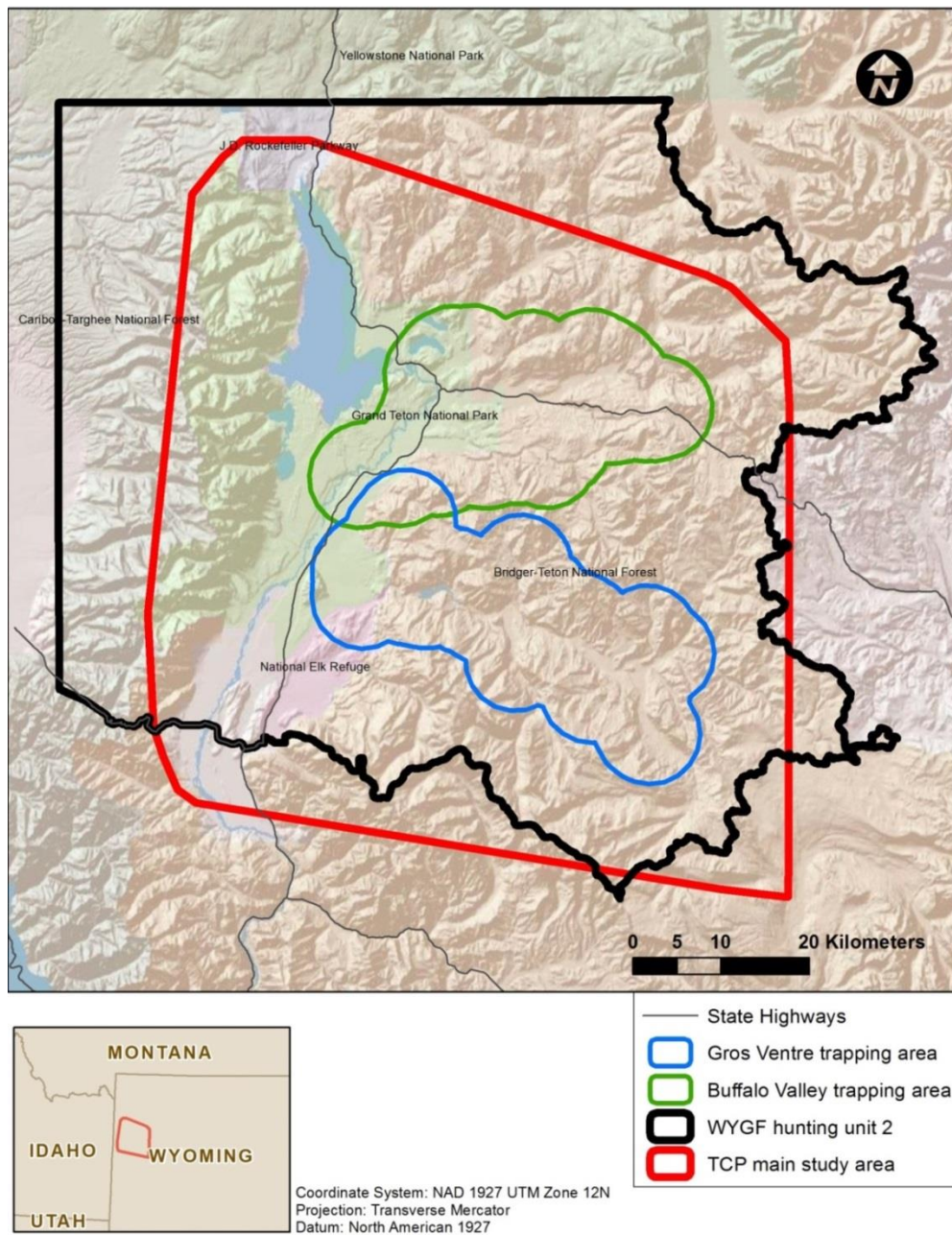


Figure 2.4. The greater study area in northwest Wyoming, represented by a minimum convex polygon of all resident cougar locations over the history of the study. Also shown is the Wyoming Game and Fish regional cougar hunting area (Hunt Area 2), and the effective trapping areas created by buffering winter track transects by the mean female home range radius.



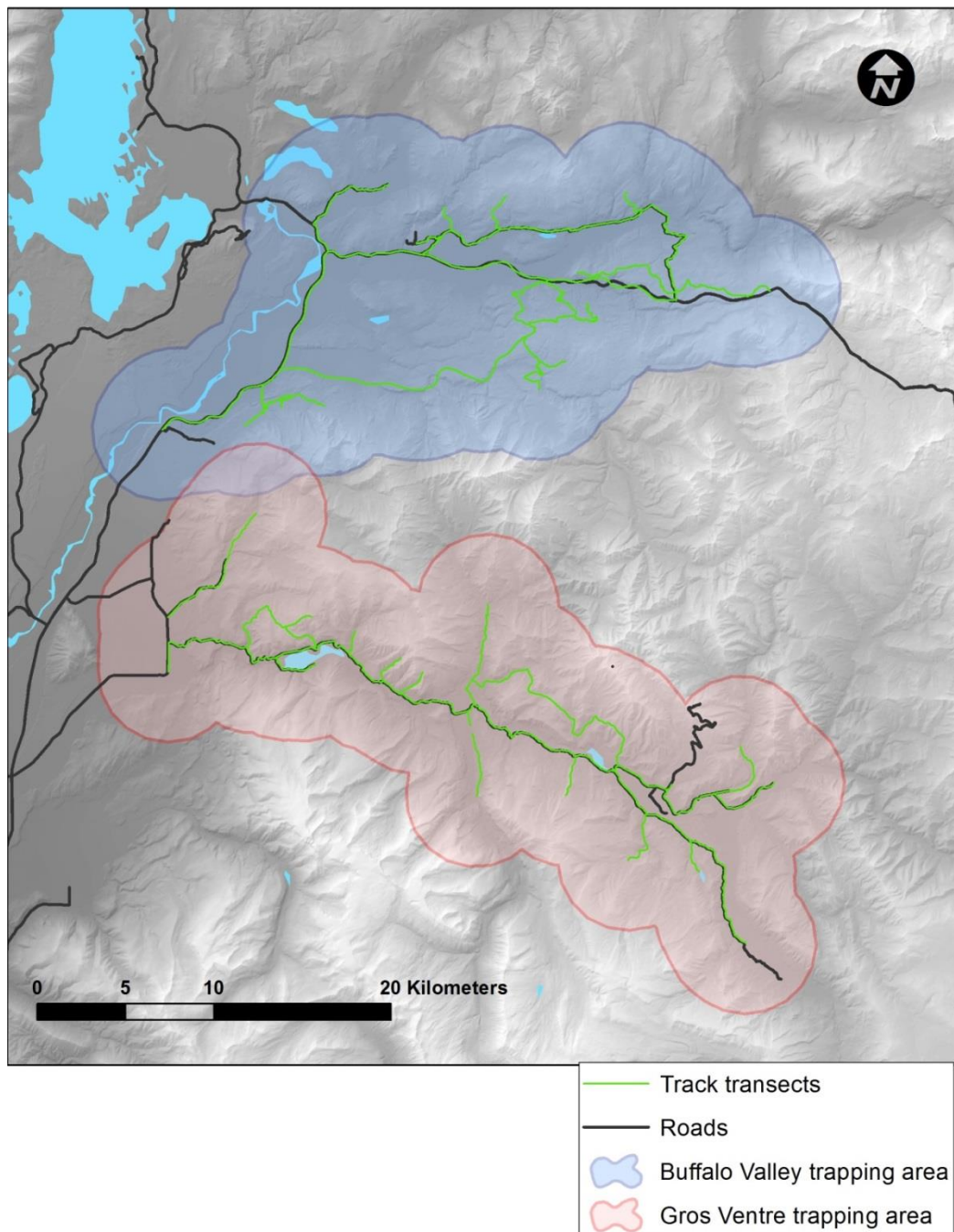


Figure 2.5. Effective cougar trapping areas around snow tracking transects in northwest Wyoming. These areas were delineated by buffering transects by average female home range radius, and used to define the area divisor, or area over which cougar density was calculated.

**CHAPTER 3**  
**A COMPARISON OF NONINVASIVE TECHNIQUES USED TO DETERMINE**  
**POPULATION DENSITY OF COUGARS**

**ABSTRACT**

Determining the size and trend of an animal population is fundamentally needed for making informed management decisions. Most carnivores, such as cougars (*Puma concolor*), occur at low densities, utilize large territories, and are behaviorally and morphologically cryptic making counting and estimation of population size extremely difficult. Consequently, most carnivores are unsuitable for conventional sight-based surveys. In addition, direct census methods involving physical capture and radio-collaring of the species are costly, invasive, and logistically challenging. Recent advances in noninvasive survey methods may offer solutions to these difficulties, but questions remain on their effectiveness and reliability. Our study objectives were to determine the density of a cougar population in northwest Wyoming using conventional capture and radio-collar methodologies, and then apply three noninvasive survey methods to the same population to evaluate and compare their accuracy and efficacy in determining population density. The noninvasive field methods included two annual sessions of 1) genetic mark-recapture using cougar hair collected from snow transects, 2) photographic mark-recapture using remote camera trapping, and 3) genetic mark-recapture using cougar scat collected with detection dogs. We used multiple types of analyses for each method, including conventional capture-mark-recapture (CMR) models, spatially explicit capture-recapture (SECR) models, and capture with replacement (CAPWIRE) models. The

reference density estimate was based on the mean count of known resident adult cougars in the study area over multiple years ( $\bar{x} = 0.82$  cougars/100 km<sup>2</sup>  $\pm$  0.10 SD; n = 3 years). We found scat detection dogs produced more plausible density estimates, were less prone to violating mark—recapture assumptions, and were more cost-effective than the other survey methods examined. The hair collection transects failed to produce a sample size large enough for a CMR abundance estimate due to poor success in field collection and genotyping. Using a SECR framework, the remote camera surveys produced a mean density estimate of 0.60 cougars/100 km<sup>2</sup> (n = 2 years; relative SD = 56.5%), and were on average 29.2% lower than the reference estimate. Only one of the two annual camera surveys produced results with confidence intervals encompassing the reference estimate. Additional analysis indicated that individual identification of cougars in photographs may not be reliable, essentially violating assumptions of tag loss and challenging the validity of photo-based population estimates of cougars. Surveys using a detection dog along transects followed by SECR analysis produced an average density of 2.41 cougars/100 km<sup>2</sup> (n = 2 years; relative SD = 12.6%). Both of the detection dog surveys produced confidence intervals encompassing the reference estimate, but density results were on average 71.8% greater than the reference estimate. Given the reference estimate was, in effect, a minimum count of known individuals, the detection dog estimates were more plausible than the underestimates produced by the remote camera surveys. The overestimation using scats found with detection dogs may be in part due to the detection of transient individuals which resulted in a high number of single detections; adjusting the timing of surveys may lessen this bias. The scat collection survey using detection dogs was also the most cost effective, with a cost-per-detection of \$341. Remote camera

surveys and hair collection transects had cost-per-detection estimates of \$3,241 and \$7,627, respectively. Our results indicate that scat detection dog surveys are more cost effective and reliable than the other methods we examined, and we recommend this method for monitoring cougar populations. Furthermore, our findings suggest that scat detection dog surveys likewise may be the most feasible method for other wide ranging carnivores with a uniform pelage.

## INTRODUCTION

Throughout the world, many carnivore populations are declining with several species becoming threatened or endangered due to a variety of reasons (Ripple et al. 2014). Accurate data on animal presence, abundance and population trends are essential for informed and effective decisions in management and conservation. In North America, cougars (*Puma concolor*) can be particularly difficult to census due to their large home range sizes, low densities, and cryptic nature (Beier and Cunningham 1996, Logan and Sweanor 2001, Choate et al. 2006). The conventional invasive method for monitoring cougar populations involve capture and radio-collaring, followed by radio-tracking to verify residency (e.g. Logan and Sweanor 2001; Cooley et al. 2009*a, b*). The resulting data can then be used in various enumerative approaches, ranging from a simple count of known individuals to determine abundance, to more precise methods using home range analyses to determine proportional residency and density (McLellan 1989, Cooley et al. 2009*a*; see Chapter 2). Although these methods have been regarded as the “gold standard” in cougar population estimation (Cougar Management Guidelines Working Group 2005), these methods are time-consuming, prohibitively expensive, and

logistically challenging. Furthermore, the process of live-capturing cougars requires direct physical contact, and can be potentially compromising to the natural behavior and health of the study animal (Proulx et al. 2012). A low-cost approach commonly used by wildlife managers is to monitor populations through data collected from hunter harvest reports and other known mortalities (Wolfe et al. 2016). While these data may provide general insights into population trends (Wolfe et al. 2016), they are affected by factors such as hunting effort and reporting rate, both of which may vary spatially and temporally in and between areas of interest (Beier and Cunningham 1996, Anderson and Lindzey 2005). Noninvasive survey techniques may offer opportunities to accurately monitor cougar population trends at a lower cost and with less impact on the study animal than conventional capture-based methods. Many carnivores are ideal for noninvasive methods due to traits such as territorial marking behaviors, inclination to respond to baited detectors due to curiosity, and scat or track morphologies unique to a species or individual (e.g. MacKay et al. 2008, Dempsey et al. 2014). The cougar's large distribution and their role as an umbrella species (Beier 2009) make them an especially attractive candidate for a cost effective method of population monitoring.

Published cougar abundance estimates using or attempting to use noninvasive methods include remote camera trapping surveys (Kelly et al. 2008, Negrões et al. 2010), DNA collection using winter track transects (Sawaya et al. 2011), hair-snares (Sawaya et al. 2011) or scat collection (Ernest et al. 2000, Davidson et al. 2014), and aerial winter track surveys (VanSickle and Lindzey 1991, Choate et al. 2006). Other methods include population indices using scent-lured track plates and ground-based winter tracking surveys (Choate et al. 2006). In our review of the literature, only the studies by Sawaya et

al. (2011) and Choate et al. (2006) were applied to marked and enumerated populations which allowed for a comparative evaluation of the noninvasive method; only the Choate et al. (2006) study attempted a comprehensive comparison of several noninvasive techniques. Based on our literature review, certain noninvasive detection techniques appeared impractical for cougars. For example, there has been little success in attracting cougars to noninvasive detectors using scent-based lures: Sawaya et al. (2011) and Choate et al. (2006) were unable to attract cougars to detectors (hair snares, and track plates, respectively) using various curiosity scents such as skunk or catnip oil. Long et al. (2003) also had little success attracting cougars to remote camera traps using similar lures; however, other studies using passive (i.e., non-baited) remote camera arrays reported practical detection rates (Kelly et al. 2008, Negrões et al. 2010). Similarly, passive genetic sampling also appeared feasible based on studies by Davidson et al. (2014) and Russell et al. (2012). Based on the studies above, we focused our research on capture-mark-recapture (CMR) analyses as opposed to population indices (Choate et al. 2006).

Noninvasive estimates of animal abundance or density are typically achieved using capture-mark-recapture based methods (also known as capture-recapture or mark-recapture; hereafter referred to as capture-mark-recapture or CMR; Otis et al. 1978, Seber 1982). There exists a wide variety of CMR-based models with different classes of statistics and various assumptions of the modeled population and trapping method, and relatively recent models have incorporated spatially-explicit data (e.g., Efford 2004, Royle et al. 2013). However, all CMR-based models are, in essence, based on refinements of the Lincoln-Peterson estimator (Kays and Slauson 2008). Traditionally,

CMR analyses require physically capturing animals, affixing a unique mark or tag before releasing them, and then carrying out subsequent captures to determine the probability of recapturing those individuals. Under a true noninvasive framework, individuals are not physically captured; they are instead effectively captured by some type of noninvasive encounter or remote detection, allowing for an already-existing and naturally-occurring mark to be recorded (hereafter we will use the terms “capture”, “encounter”, and “detect” interchangeably). These natural marks can be any physical or genotypic trait, as long as that trait is unique to the individual and reliably recognizable with whatever subsequent detection method is used. The resulting capture history of noninvasive captures and recaptures is recorded and analyzed similarly to traditional CMR methods (e.g., Karanth 1995, Wasser et al. 2004).

Among other model assumptions (Williams et al. 2002), conventional CMR analyses generally require population closure (i.e., the demographics of a surveyed population are assumed to remain constant during a sampling period with no births, deaths, immigration or emigration). Cougars, consequently, are particularly problematic due to their year-round potential for breeding and dispersal. Ostensibly, the observed increase in denning and dispersal during summer months (Logan and Sweanor 2010, Ruth et al. 2011), would aid in reducing closure issues when surveys are timed accordingly. However, this is somewhat negated since cougars often exhibit a semi-independent stage before full independence and dispersal (Quigley and Hornocker 2010). Population closure issues are further exasperated in areas with high hunting mortality (e.g., Cooley et al. 2009*a, b*). Due to these uncertainties, survey methods using

temporally short sampling periods are generally recommended to reduce closure issues (Harihar et al. 2009).

Further underpinning the uncertainties of closure is the problem of spatial scale. Spatial scale is a frequently cited issue for estimates of population density (Efford 2004). As with traditional trap arrays, the area that is effectively trapped around noninvasive detectors (i.e., remote cameras or sampling transects) is difficult to quantify (Wilson and Anderson 1985, Efford 2004, Royle et al. 2013). This can be considered an issue of population closure since individuals residing on the edge of a trapping grid are, effectively, temporary immigrants and emigrants (Kendall et al. 1997). This may be especially applicable to cougars due to their large home ranges. A commonly used method for determining the effective trapping area is to spatially buffer the trap array by some distance, under the assumption the buffer would include any animals that could be captured by the trapping array. Often, one half of the average home range diameter of the study animal was used to determine the buffer distance (Dice 1938, Karanth and Nichols 1998). Radio-telemetry data may not be available for determining average home range size; it was instead determined by proxy using an individuals' detection locations on the detector array to measure the mean maximum distance moved (MMDM; Wilson and Anderson 1985, Karanth and Nichols 1998). Jaguar research by Soisalo and Cavalcanti (2006) compared the MMDM derived from camera detections to home ranges determined from GPS telemetry, and reported the MMDM method significantly underestimated the distances actually moved by jaguars on the trapping array. Using the incorrect measure of MMDM created an underestimated effective trapping area, and thus inflated density



estimates (Soisalo and Cavalcanti 2006). This error in spatial extent could likely affect density estimates for other animals with large home ranges, including cougars.

A relatively recent solution to the issue of spatial uncertainty in CMR models is spatially explicit capture-recapture models (SECR; Efford 2004, Royle et al. 2013). These models incorporate the locations of detections into the capture history, resulting in a spatially-explicit abundance estimate by which density is directly parameterized. In general, SECR models use a hierarchical framework to calculate the probability of detection as a function of the distance of an individual's home range center to a detector (Efford 2004, Royle et al. 2013). SECR models have been employed for cougar density estimates in scat detection dog surveys (Davidson et al. 2014) and winter hair collection surveys (Russell et al. 2012). SECR is advantageous since it eliminates the ad hoc spatiality, thereby eliminating the need for a trap buffer and somewhat relaxes the assumption of population closure (Gardner et al. 2009). However, this relaxed assumption is likely more applicable to the temporary emigrant/immigrant scenario outlined above, as opposed to completely transient individuals that do not have a home range to be modeled. Therefore, a survey method with a brief sampling period is likely still prudent.

### **Photographic Mark Recapture**

Automatically triggered cameras have been used in wildlife research since as early as the 1920s when biologists used them to document species presence and richness. However, their use was somewhat limited until the 1980s when relatively inexpensive camera units using motion sensor technology became available (Kays and Slauson 2008). In the 1990s, studies began using large arrays of motion sensor cameras to estimate

population size for difficult-to-observe species such as grizzlies (*Ursus arctos*; Mace et al. 1994) and tigers (*Panthera tigris*; Karanth 1995). Tigers, having a unique pelage for each individual, were ideal for modern CMR methods since individuals could be confidently identified in photographs without the need for artificial tags (Karanth 1995). An important assumption of CMR models is that once captured and tagged, individual animals are dependably recognized in subsequent captures (Seber 1982). Since tigers are naturally “marked”, photographic captures and subsequent re-captures of the same individual can be identified (Karanth 1995). However, there has been some debate as to whether species without obvious markings, such as cougars, can be reliably identified at the individual level in photographs, thereby respecting the identifiable marks assumption (Kays and Slauson 2008, Kelly et al. 2008). Some studies have estimated cougar population size using remote camera trapping without artificial marks (e.g., Kelly et al. 2008, Negrões et al. 2010, Soria-Díaz et al. 2010). These studies argued that individual cougars could indeed be reliably identified by natural pelage markings, scarring, or morphology, and therefore qualified to perform CMR analysis. The work by Kelly et al. (2008) specifically examined the extent to which independent investigators agreed with one another when identifying individual cougars in remote camera images, and found 72.9% average agreement between three independent investigator teams. However, research on individual identifiability of other animals with a uniform pelage (Yoshizaki et al. 2009, Oliveira-Santos et al. 2010) suggested that even small discrepancies in encounter histories created large variances in the resulting abundance estimate, and stressed caution if relying on this type of identifying mark. Furthermore, investigators may identify cougars using physical traits that, while distinctive, may not be unique (e.g.,

a kinked tail or missing ear). Consequently, as a sample size increases, the likelihood of multiple cougars with the same trait would also increase (Harmsen 2006), thereby increasing the potential for misidentification.

### **Genetic Mark Recapture**

Genetic CMR uses DNA as a captured individual's identifying mark. In recent decades, technological advances in molecular biology and genetics have given researchers access to these methods at relatively low cost (Parker et al. 1998). Noninvasive sampling techniques typically focus on scat or hair that has been deposited by an animal, either naturally or at a predetermined sampling site using an attractant. Examples include using trained dogs to locate and collect grizzly bear scat (Wasser et al. 2004), or setting up hair snares for black bears (*U. americanus*) and grizzly bears (Woods et al. 1999). Samples are then genotyped to determine the individual identity using polymerase chain reaction (PCR) and microsatellite analysis (Schwartz and Monfort 2008), which are then incorporated in the capture history and subsequent CMR analysis. An important drawback to these methods is that DNA analysis cannot currently provide information on a detected individual's age (Schwartz and Monfort 2008) or known fate (i.e., death or dispersal). Uncertainty in age is problematic for genetic surveys of cougar populations, since cougar offspring may remain dependent members of a family group as late as two years old (Quigley and Hornocker 2010). Consequently, a noninvasive genetic survey would not be able to differentiate members of a single family group from multiple independent adults. Depending on research focus and scope, distinguishing these age classes may not be important to management decisions, since female kill rate increases when caring for dependent young (Knopff et al. 2010), and thereby kittens can play an

influential ecological role. However, this uncertainty in age class likely biases CMR analyses due to heterogeneity in detection probability between dependent kittens and adults: since mother cougars will typically spend part of their time hunting or traveling without their kittens, kittens likely have a lower probability of detection than adults (Logan and Sweanor 2001, Davidson et al. 2014). Since age class is unknown in a capture history, this heterogeneity cannot be explicitly modeled as a covariate into a CMR abundance estimate. Furthermore, as kittens grow older, this heterogeneity likely changes over a relatively short amount of time, potentially within the temporal sample period of a multi-sample genetic survey. It is worth noting that this issue may soon be resolved due to research on chromosomal telomere shortening as a function of aging (Nakagawa et al. 2004), which may allow for the age of an individual to be reliably determined from a genetic sample.

*Genetic CMR via snow tracking for hair samples.*— Hair collection has likely been used to identify species presence for millennia (Kendall and McKelvey 2008), but only with relatively recent technological advances in molecular biology have researchers been able to discern individual identity from hair, thus allowing for genetic CMR analysis. Kendall and McKelvey (2008) divided hair collection methods into two basic categories: baited and passive. Whereas baited methodology involves an attractant and usually some type of collector (i.e., a hair snare), passive hair collection attempts to locate hair naturally shed by the study animal. Both categories have advantages and disadvantages depending on the traits of the study animal and accepted level of invasiveness. In cougar research, however, researchers have had little success with baited hair snares (Choate et al. 2006, Sawaya et al. 2011). Sawaya et al. (2011) and Russell et

al. (2012) used a passive method of following cougar tracks in snow to find and collect hair naturally deposited at bedsites and natural vegetative snags. Kendall and McKelvey (2008) stressed caution, as extracting DNA from hair at the quality sufficient for determining individual identity was difficult, and different species likely shed DNA at different rates (Goossens et al. 1998). Felids, in particular, shed low amounts of DNA with hair as compared to other carnivores (Kendall and McKelvey 2008). Since there was little to no genetic material in a hair shaft, extraction success was dependent on follicles being present in the sample (Goossens et al. 1998). Cougars may not regularly shed hair that includes follicles, and follicle presence in a sample may not be easily discerned by investigators in the field. Russell et al. (2012) and Sawaya et al. (2011) reported between 13% and 39% success rate for successful DNA extraction from hair to the individual level, suggesting that a relatively large sample was required for successful abundance estimates.

*Genetic CMR via scat detection dogs.*— Scat is probably the most abundant animal byproduct collected noninvasively and used for genetic analysis (Wasser et al. 2004). Genetic analysis of scat is dependent on sloughed epithelial cells from the digestive tract, which remain on scat after being defecated. Careful collection and extraction of scats can produce high quality DNA markers usable for individual identification (Schwartz and Monfort 2008). However, locating scat from cryptic and sparsely occurring species such as cougars is often difficult (Harmsen et al. 2010). A common solution is the use of scat detection dogs (also known as scat dogs or conservation dogs). Domestic dogs (*Canis familiaris*) have highly sensitive olfactory systems relative to that of humans. Combined with their trainability, these traits have

long been exploited by humans. Since as early as the 1800s, wildlife biologists have used dogs for the detection of wildlife or wildlife sign (Mackay et al. 2008). In recent years, researchers have been able to incorporate detection dogs with genetic analysis (e.g., Smith et al. 2003, 2005). Davidson et al. (2014) estimated the density of a cougar population in Oregon using this method, and found comparable density estimates using several CMR-based models. Davidson et al. (2014) was not able to evaluate their result with a direct enumerative estimate. One disadvantage to scat surveys relates to the uncertainty of the temporal sampling window. Typically, trapping surveys (including remote camera surveys) have distinct timeframes of capture. Likewise, genetic surveys collecting samples from a target species' tracks in snow or a baited hair-snare will have a temporal window within which the individual was known to be present. However, there may not be information about the length of time a scat on a passive transect is detectable, creating uncertainty in the sampling window, and potentially violating assumptions of population closure. One solution is to initially "clean" (i.e., collect and discard) scats along transects before subsequent transects. However, financial cost may prohibit multiple transect visits. An upper limit to the sampling window is likely determinable by genotyping success: Lonsinger et al. (2015) found PCR success for scat samples collected from coyotes (*Canis latrans*) and kit foxes (*Vulpes macrotis*) was dependent on the age of scat, among other factors. For their target species, PCR success rates dropped below 50% after 7-21 days. However, there was also a significant difference in PCR success rates between the two canid species, and applying their findings to another species is not necessarily appropriate. Similar research on cougar scat might provide a reliable scat degradation timeframe, outside of which PCR failure would prevent samples from being

incorporated into a genetic detection history regardless of their being detected and collected in the field.

Our study objectives were to determine the density of a cougar population in northwest Wyoming using conventional capture and radio-collar methods (i.e., invasive method), and then apply three noninvasive survey methods to the same population and area to evaluate and compare their accuracy and efficacy in determining population density. The noninvasive field methods included two annual sessions of a) genetic mark-recapture using cougar hair collected from snow transects, b) photographic mark-recapture using remote camera trapping, and c) genetic mark-recapture using cougar scat collected with detection dogs. We used multiple types of analyses for each method, including conventional capture-mark-recapture (CMR) models, spatially explicit capture-recapture (SECR) models, and capture with replacement (CAPWIRE) to determine population size and density.

## **STUDY AREA**

The study area encompassed ~5,120 km<sup>2</sup>, including much of the Jackson Hole basin and adjacent lands in northwest Wyoming. The area was delineated by the Teton Range in Grand Teton National Park (GTNP) on the west, the Gros Ventre Range on the east, the Teton Wilderness Area on the north, and on the south by Wyoming state highway 22 and the Cache Creek drainage (Fig. 3.1). Most lands within the study area were administered by the U.S. Forest Service (Bridger-Teton National Forest), the National Park Service (Grand Teton National Park), and U.S. Fish and Wildlife Service (National Elk Refuge). A small percentage (~ 5%) was privately owned ranches or

residential areas. Elevations in the study area ranged from ~1,800 m in the Jackson Hole basin to >3,600 m in the mountains. The area was characterized by short, cool summers and long winters with frequent snowstorms. Average monthly temperature minimums and maximums ranged from -17.3°C and -3.4°C in January, to 5.3°C and 26.9°C in July. Precipitation occurred mostly as snow, and mean maximum snow depths ranged from 100 cm at lower elevations to >245 cm at intermediate elevations of 2,000 – 2,400 m (Grand Teton National Park 2015).

Plant communities included cottonwood (*Populus angustifolia*) riparian zones interspersed by sagebrush (*Artemisia spp.*) uplands at lower elevations. At intermediate elevations, aspen (*P. tremuloides*), Douglas-fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*) were the dominant species. Spruce (*Picea engelmannii*) and fir (*Abies lasiocarpa*) were the primary tree species at higher elevations (Marston and Anderson 1991, Knight 1996).

Primary prey species available to cougars included mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), white-tailed deer (*O. virginianus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and various small to medium sized mammal and avian species. The study area also included all historically occurring carnivores: grizzly bears, black bears, and gray wolves (*Canis lupus*), as well as coyotes and red foxes (*Vulpes vulpes*), and possibly bobcats (*Lynx rufus*) and lynx (*Lynx canadensis*).

## METHODS

Our research was part of a long-term cougar ecology study in northwestern Wyoming that incorporated the capture and GPS-tracking of resident adult cougars. We



previously reviewed various methods to enumerate cougars in a defined area (Chapter 2). We then determined an estimate of density for the core region of the study area, delineated by the effective trapping area or “area divisor”. Our method used GPS-telemetry data to enumerate the proportional residency of cougars in the area divisor (McLellan 1989, Cooley et al. 2009a) for the years 2011, 2012, and 2013 (defined annually as Sept 1 – Aug 31). We also included detected-but-unmarked cougars (based on remote video and photo detections) when residency could be confidently assigned, and backlogged subsequently captured cougars to previous years based on age and sex (Logan and Sweanor 2001). Density estimates were scaled to cougars per 100 km<sup>2</sup>. The mean of these density estimates constituted our reference estimate to which we compared the noninvasive results.

We delineated the noninvasive survey areas to correspond approximately with the area divisor from Chapter 2 (Fig. 3.2). These survey areas encompassed ~1,600 km<sup>2</sup>, and, as with the area divisor, were defined generally by the Gros Ventre and Buffalo Valley drainages where the majority of cougar detection and trapping efforts occurred. Over the history of the long-term cougar ecology study (2001 – 2013), 93% of cougar capture locations (n = 154 cougars) and 80% of GPS telemetry locations (n = 47,563 locations) occurred within this core area. We employed three types of noninvasive surveys: remote camera surveys, winter tracking for genetic sampling, and genetic sampling using scat-detection dogs. We limited our CMR analyses to relatively well known methods that were readily accessible to wildlife managers.

*Cost comparison.*— We compared the resource requirements of each survey type using the rate of animal detection as the unit of measure. We only included detections

used in final population estimates (i.e., genetic samples that were collected but did not yield individual identity did not count in the cost analysis). We calculated cost-per-detection in dollars, and effort-per-detection in person-days of labor. We estimated the true costs of donated equipment and volunteer labor to the best of our knowledge, referencing similar, commercially available equipment or median salaries for comparable positions (Bureau of Labor Statistics 2015)

*Detections of radio-collared cougars.*— CMR analysis produced estimates of detection probability for each survey; we also produced alternate estimates of detection probabilities based on noninvasive detection of radio-collared individuals. We applied a simple two-sample Lincoln Peterson estimator (Krebs 2001), using the Chapman estimator for small samples (Chapman 1951). We used captured and radio-collared animals as the first sample, and noninvasive survey detections as the second sample:

$$\hat{N} = \left( \frac{(n_1 + 1)(n_2 + 1)}{m_2 + 1} \right) - 1$$

where  $\hat{N}$  is the abundance estimate,  $n_1$  and  $n_2$  are animals captured or detected in the two sampling sessions, and  $m_2$  is the number of radio-collared animals detected in the second sample. We then solved for  $\hat{p}$  using the formula:

$$p_i = \frac{C_i}{\hat{N}}$$

where  $p$  is the probability of detection,  $C$  is the number of animals detected, and  $i$  is the sample occasion.

We also examined detection success using Poisson regression analysis to examine the number of detections of radio-collared cougars as a function of density of detectors per individual home range. Density of detector  $dd_i$  was defined for cameras as the number of camera stations per  $\text{km}^2$  of home range  $i$  (defined by 95% kernel density estimation; see Chapter 2). For transect based surveys, we measured  $dd_i$  by kilometers surveyed per  $\text{km}^2$  of home range  $i$ . Home ranges were delineated annually by 95% KDE (see Chapter 2 for details on home range calculation).

### **Photographic Sampling**

*Field methods.*— We established an array of remote cameras stations across the core study area during the summer months of 2012 and 2013, using two types of camera station design. The majority of sites ( $n = 43$ ) used a blood-based non-reward lure; the remaining sites ( $n = 10$  in 2012;  $n = 12$  in 2013) were set up using conventional camera survey methods with cameras placed along high-use trails (e.g., Karanth 1995, Negrões et al. 2010). For the blood-lure stations, we first divided the core study area (described above) into  $36 \text{ km}^2$  cells. This cell size was based on the low densities of the target animal (Rovero et al. 2013), and chosen so an average home-range size of a female cougar would overlap the spatial equivalent of four cells. This resulted in 43 contiguous sampling cells covering  $1,548 \text{ km}^2$ , divided between the Gros Ventre ( $n = 21$  sampling cells) and Buffalo Valley ( $n = 22$  sampling cells) drainages. One camera station was setup for each cell. Camera stations were active from approximately June 15 to September 15 for each year. We selected the exact locations of the camera stations within

each cell based on topographic or vegetative features typical of cougar habitat or travel routes. These sites were typically characterized by ridgelines, drainage bottoms, or edge habitat where cougars were either known (via telemetry or natural sign) or suspected to travel (Fig. 3.2). Due to our choice of blood-based attractant (see below) and the potential for human-bear conflict, we were restricted from placing camera stations near roads, human development, or high-use trails where humans regularly traveled. We installed two models of motion-activated cameras at each station. The first type was a non-commercial model designed by Panthera (Panthera Inc., New York, NY), which used a visual-light xenon flash for nighttime images. The second camera type was a commercially available infrared model: either the Reconyx PC800 or Reconyx Silent Image (Reconyx, Inc., Holmen, WI). All camera models used a passive infrared sensor for motion-triggered activation. The Reconyx camera used infrared lighting at night, which resulted in black and white images. The Panthera model always used visual light, either from ambient daytime light or from the xenon flash, and thus produced color images. The xenon flash was relatively slow to recharge, so the Panthera cameras generally produced fewer night images than the Reconyx cameras. We fixed the cameras to tree trunks approximately 50 to 80 cm off the ground and 10-15 m apart, with both cameras aimed in a manner to capture two sides of an animal as it passed through the site. We placed an 80 cm high wood post between the cameras marked at 10 cm increments to help estimate animal height and aid in individual identification (Fig. 3.3). To increase detection probability and number of photos per event, we used a non-reward lure comprised of aged cattle blood. This type of attractant was chosen based the low success rate of non-food based scent attractants reported by Long et al. (2003), Choate et al.

(2006), and Sawaya et al. (2011), and anecdotal evidence that cougars responded to blood-based attractants at grizzly bear trapping sites (D. Thompson, Wyoming Game and Fish Department, pers. comm.). The lure was suspended in an open container (a repurposed laundry detergent jug) between trees by rope at least 4 m above the ground, directly above the measurement post. Sodium citrate was mixed with the blood to prevent coagulating and thus retain odor (Haroldson and Anderson 1996). We also suspended a repurposed compact-disc to act as a visual attractor. We use the terms “lure” and “attractant” loosely, in that the blood mixture and the compact disc were used in order to provoke the curiosity of any cougar already passing through the area, as opposed to attracting cougars from large distances. We hoped this would in turn generate a maximum number of photos, based on the assumption that additional photos would increase our ability to individually identify cougars.

The second type of camera station (hereafter referred to as “trail camera stations”) was setup at an additional 10 -12 sites. The trail camera stations were setup as a method to compare detection rates of our novel blood-lure technique with the conventional placement method used in other cougar camera trapping studies (e.g., Kelly et al. 2008, Negrões et al. 2010). These trail cameras used a single Panthera or Reconyx camera, fixed approximately 50 to 80 cm off the ground. A small amount of cologne-based lure comprised of “Calvin Klein Obsession for Men” (Calvin Klein Inc., New York City, NY) and synthetic civet musk or catnip oil (Grawe’s Lures, Wahpeton, ND) was placed in front of the camera. Field crews visited stations at a minimum of every two weeks to download images and perform any needed site maintenance. We replenished the blood lure every 4 weeks, or as needed.

*Density estimate.*— Photographic captures of cougars at camera stations were cataloged as “events” and generally consisted of multiple, sequential images of the captured individual. Events were considered separate if >6 hours elapsed between photos of the same cougar. We identified and distinguished individual cougars in photographs based on artificial tags, physical features (i.e., kinked tails, pelage markings, facial features, or size), and spatial/temporal distance between detections. We used resulting capture data to run conventional closed capture models (Otis et al. 1978; see Karanth 1995, Kelly et al. 2008) and spatially explicit capture-recapture methods (SECR; Efford 2004, Royle and Nichols 2009) to calculate densities, both separately and together for the Buffalo Valley and the Gros Ventre drainages.

For the conventional closed model, we used program MARK (White 2008), implemented through the R package RMark (Laake and Rexstad 2008). Detections were organized into capture histories of 8 occasions. In order to calculate density estimates, we estimated the effective trapping area of the camera station array by buffering camera station locations by the average female home range radius (analogous to the commonly used MMDM metric; see Soisalo and Cavalcanti (2006); see Chapter 2). To calculate the buffer distance, we calculated female home ranges during the remote camera survey months (June – September) from all GPS-collar data spanning the history of the study. Home ranges were only calculated if the individual’s seasonal home range was comprised of a minimum of 50 relocations, as recommended by Seaman et al. (1999), and incorporated a minimum of 100 days. Home ranges were defined by 95% kernel density estimation (KDE) using the plug-in bandwidth (Jones et al. 1996). We used the geometric radius of the average female seasonal home range, weighted by individual, to determine

the buffering distance. All spatial analyses were completed in the R programming environment (R Version 3.0, [www.r-project.org](http://www.r-project.org), accessed 10 Oct 2013), using the *adehabitat* package (Calenge 2011) and the *ks* package (Duong 2014), as outlined by Walter and Fischer (2015). We also used the R packages *maptools* (Roger et al. 2014), *rgeos* (Bivand and Rundel 2011), and *shapefiles* (Stabler 2014) to construct trapping buffers. Visualization of processes were implemented in ArcMap 10.2 (Environmental Systems Resource Institute 2013).

To estimate density directly, we used a Bayesian inference model designed for mark-recapture studies (Royle et al. 2009) in the R package SPACECAP (Gopalaswamy et al. 2012a). SPACECAP is designed specifically for noninvasive surveys with a user-friendly platform with a graphical user interface. SPACECAP has been used to estimate density for other elusive felids using remote camera surveys, including leopards (*Panthera pardus fusca*; Thapa et al. 2014), Scottish wildcats (*Felis silvestris silvestris*; Kilshaw et al. 2014), and Amur tigers (*Panthera tigris altaica*; Hernandez-Blanco et al. 2013). SPACECAP employs Bayesian inference by Markov chain Monte Carlo (MCMC) methods, using the Metropolis algorithm (Gelman et al. 1996) to estimate parameters: notably density  $D$ , probability of detection at an individual's home range center  $\lambda_0$ , and a measure of an individual's home range size as probability of detection decreases towards zero  $\sigma$ . The model used by SPACECAP applies to binary observations  $y(i,j,k)$  for individual  $i$ , trap  $j$ , and sample occasion  $k$ . The model is a binary regression model in which  $y(i,j,k) \sim \text{Bernoulli}(p(i,j,k))$ , where  $p$  is the probability of detection; see Gopalaswamy et al. (2012a) and Royle et al. (2009) for more information on the modeling details. We input encounter histories, camera station locations, and a spatial

mask layer of potential home range centers representing the state-space  $S$ . Since spatially explicit models incorporate trap location, we ran the SPACECAP models using the additional trail camera detections despite the non-uniform trap spacing that would not have been suitable for conventional CMR models. The mask layer was a grid of points spaced evenly at 2,236 m, with each point representing a “pixel” of 5 km<sup>2</sup>. SPACECAP produced an estimated density at each pixel. Pixel size was approximately 1/32<sup>nd</sup> of the target animal’s home range, following protocols suggested by Gopalaswamy et al. (2012b). The state-space  $S$  extended 20 km around the camera station array, in order that it included all potentially existing cougar home ranges that could be detected at camera stations (see below for details on delineation of state-space). We extracted a canopy cover value to the mask layer, and assigned ‘1’ to all points that had no canopy cover (defined as percent canopy cover <1%), effectively eliminating open water and open sage habitats from the array of potential home range centers. We ran models with and without a behavioral trap response. SPACECAP allows for two types of detections functions: half-normal and the negative-exponential. We used the default half-normal function (see below for details on detection function selection). We performed a minimum of 200,000 MCMC iterations with a burn-in period of 50,000, and a thinning rate of 1 for each model. Iterations and burn-in were increased if models did not perform adequately. Model convergence was evaluated using the Geweke diagnostic statistic (Geweke et al. 1997), with  $z$ -scores between -1.6 and 1.6 indicating reasonable model performance. Model fit was evaluated using the Bayesian P-value (Royle et al. 2011), with values close to 0 or 1 indicating poor model fit. Models were also evaluated with a measure of



effective MCMC sample size adjusted for auto-correlation (Martyn et al. 2015). All evaluators were calculated within the SPACECAP platform.

*Selection of detection function and delineation of state-space.*— To evaluate the appropriateness of SPACECAP's available detection functions, we plotted the density of cougar locations as a function of distance from home range center. We performed this using the R packages *maptools* (Bivand and Lewin-Koh 2014), *rgeos* (Bivand and Rundel 2011), *raster* (Mattiuzzi et al. 2015) and *unmarked* (Fiske and Chandler 2011). We first separated all available GPS locations by individual and year (as defined by remote camera survey months June 15 to September 15). Remaining location sets were discarded if the number of locations was <50 and the time range was <30 days. We assumed an unprojected Cartesian coordinate system and re-referenced each location set around its geometric center defined as  $x = 0$  and  $y = 0$ . We combined all re-referenced location sets and extracted distance-to-center for each GPS location (Fig. 3.4). The resulting density plot suggested that the half-normal detection was more appropriate than the negative exponential (Fig. 3.5). The density plot also suggested a low likelihood of encountering a cougar further than 20 km from its home range center, and we delineated the state-space  $S$  accordingly.

*Reliability of identifying individual cougars in photographs.*— Unlike certain other large felids, cougars do not exhibit unique pelage markings and there is some debate whether cougars are appropriate for photographic CMR methods (Kelly et al. 2008, Oliveira-Santos et al. 2010). Reliably identifying individual cougars in photo-captures was an important component of our measure of feasibility; however, our results were likely biased in this regard since at least a portion of the target population was

visually identifiable due to GPS-collars and ear tags. To examine the issue of identifiability in an uncollared population, we tested the agreement to which independent investigators distinguished individual cougars in our photographic captures without the aid of artificial marks. We designed a photo database and electronic form in Microsoft Access (Microsoft Corporation, Redmond, WA) that allowed independent investigator participants to sort through photographic capture events and assign individual identity. We selected a subsample of events from the 2013 survey, which included events from both camera station designs. To create the subsample, we discarded events that had radio-collared cougars or very poor photo quality. The Access form displayed events in pairs, with an event displayed on each side of the computer monitor. The form allowed investigators to scan through events on each side independently, as well as to sort through the multiple images associated with each event (Fig. 3.6). For each event pairing, the investigator was prompted to classify the pair as being from the same individual cougar, or two different cougars. Also included were spatial and temporal data for each event, with the spatial and temporal separation between the paired events automatically calculated and displayed (e.g., “events A and B were 10.5 km and 51.3 hours apart”). We considered this information “fair game”, because we believed these data would logically be included in a similar real-world research scenario, and should therefore not be ignored. All combinations of event pairings were evaluated. Note that this method can result in a large sample if a sufficient number of events are compared:

$$C = \frac{n!}{2!(n-2)!}$$

where  $C$  is the number of combinations to evaluate, and  $n$  is the number of events.

We distributed the Access database to independent participants. Only wildlife researchers with considerable experience with cougars were considered for participation.

A segment of the participants included biologists who performed cougar research in the study area and were familiar with the individual cougars in the photo database.

Participants were not privy to our own identification assessment, capture history, or CMR results. We used the R package *irr* (Gamer et al. 2014) to calculate agreement level. We used simple percent agreement, similar to the metric that Kelly et al. (2008) used, as well as Fleiss's kappa (Fleiss 1971). We included Fleiss's kappa as it was a more statistically rigorous metric of agreement between assessors than simple percent agreement (Gwet 2010). A kappa of 1 indicated perfect agreement, and 0 indicated a level of agreement consistent with completely random assessments by participants. We stress the above analysis was not intended to confirm whether participants were correct in their assessment of individual cougar identity; our goal was to test for disagreement, thereby suggesting photographic CMR results may not be suitable for cougars due to an inability to reliably identify individuals. We also examined our hypothesis that a greater number of photos per detection would increase our ability to identify individuals. We used Poisson regression to examine the count of participants in agreement for each event pairing as a function of the total number of photos in the event matching.

### **Genetic Sampling**

*Field methods for winter tracking transects.*— We delineated 226 km of transects across the study area, split between the Buffalo Valley (54%) and the Gros Ventre (46%) drainages. Transects were performed during the winters of 2011-2012 and 2012-2013.

Transects were performed by truck (21%), snowmobile (60%), or on snowshoes/skis (19%). Transects were selected based on topographic features characteristic of cougar habitat or travel routes, and ease of access for trackers (Fig. 3.2). Transects were the same routes that were used for detecting and capturing study animals for radio-collaring (see Chapter 2). Snowshoe/ski transects were typically characterized by ridgelines, drainage bottoms, or edge habitat where cougars were either known (via telemetry) or suspected to use. Truck and snowmobile transects were based additionally on accessibility and ability of researchers to quickly transect large amounts of terrain. We attempted to schedule transects at least 24 hours after a snowfall, but not later than 72 hours. This schedule was chosen in order to maximize the sampling window of time when cougars were potentially traveling, without compromising an observer's ability to detect tracks due to being obscured by other animal tracks or wind/weather. When cougar tracks were detected, researchers backtracked (or forward tracked if backtracking was not feasible) until a genetic sample (either hair or scat) could be collected. Hair was collected at bedsites, vegetative snags, or within tracks. We followed general collection recommendations outlined by Schwartz and Monfort (2008). To avoid genetic cross-contamination, each sample was collected using fresh latex gloves and sterilized thumb forceps. Hair samples were stored in small paper envelopes, which were then placed in 50 mL plastic FALCON® tubes, each with approximately 20 mL of silica gel. Scat samples were collected in unused "ziplock" type bags with silica gel (silica gel was added at approximately 2 times the estimated weight of the scat sample). All samples were stored out of direct sunlight at room temperature before being transferred to a laboratory for genetic analysis.

*Field methods for scat detection dogs.*— We used a single handler/dog team (Find It Detection Dogs, Walden, CO) to survey 20 transects across the core study area, divided between the Buffalo Valley ( $n = 8$ ) and Gros Ventre ( $n = 12$ ) drainages. Transects were run in late summer of 2013 and 2014. Transects were chosen based on terrain features characteristic of cougar habitat (similar to winter track transect selection described below), as well as accessibility. Detection dogs were restricted from entering Grand Teton National Park, which limited our ability to run transects in certain areas in the western portion of the area divisor (see Chapter 2). The initial transect delineations were course and approximate; these course transect lengths totaled 140 km (55 km in the Buffalo Valley drainage; 85 km in the Gros Ventre drainage), with an average transect length of 7.0 km. The dog handler team followed these transects using a handheld GPS device, but was given flexibility to choose exact routes while in the field (Fig. 3.2). Dogs were primarily trained using cougar scat collected from other regions, with a “refresher” training using locally collected scat performed immediately prior to our survey. Detection dogs were trained to walk off leash while searching for cougar scat, staying within approximately 25 m of the handler. When scat was detected, dogs were trained to signal the handler without touching the scat, allowing the handler to approach and verify. Unless scat was unmistakably a non-target species, all scat indicated by the dog was assumed to be cougar. Scat was sampled using sterile thumb forceps to collect approximately 0.5 mL of fecal material from the outside of the scat (Stenglein et al. 2010). The sample was placed in a 2 mL screw-top plastic tube containing 1.5 mL of DET buffer (Davidson et al. 2014), and agitated to saturate the sample. We stored

samples at room temperature and out of direct sunlight until transferring them to a genetics laboratory.

*DNA extraction and analysis.*— Analysis of genetic samples was split between two labs depending on the year of collection. Hair samples and scat samples collected in 2013 were analyzed at the Sackler Institute for Comparative Genomics (Center for Conservation Genetics, American Museum of Natural History, New York) as follows: genomic DNA from scat samples was extracted using the QIAmp DNA Stool Mini Kit (QIAGEN, Valencia, California) with modifications as outlined in Caragiulo et al. (2013). Genomic DNA from hair was extracted with the DNeasy Blood and Tissue Kit (QIAGEN, Valencia, California), using the manufacturer's recommended protocols. All samples were initially tested for species identification as described in Caragiulo et al. (2014), and screened out of further analysis if not identified as cougar. We used 21 cougar specific microsatellite primers which were developed by Kurushima et al. (2006). Polymerase chain reactions (PCR) were carried out in 12.5  $\mu$ L multiplex reactions containing 2 to 5  $\mu$ L of extracted DNA, 0.65  $\mu$ L of each forward and reverse 10  $\mu$ M primer, and 5  $\mu$ L Qiagen Mutlplex PCR Master Mix, 1  $\mu$ L Q-solution, and the remaining volume was RNase-Free water (QIAGEN, Valencia, California, USA). We grouped primers into four multiplex reactions based on fluorescent tag and amplicon size. Thermocycling conditions were the same for all primers and multiplexes: initial denaturation for 15 minutes at 95 °C, 13 cycles of denaturation at 94 °C for 30 seconds, annealing with touchdown at 62.4 -0.3 °C for 90 seconds, and elongation at 72 °C for 60 seconds, followed by 32 cycles of denaturation at 94 °C for 30 seconds, annealing at 60 °C for 90 seconds, and elongation at 72 °C for 60 seconds, followed by a final elongation

at 60 °C for 30 minutes. We prepared samples for analysis by mixing 1 µL of PCR product with 9 µL of an 8.82 µL: 0.18 µL mixture of Hi-Di formamide: GeneScan 500 LIZ size standard (Applied Biosystems, Carlsbad, California, USA). Samples were heat-shocked for 3 minutes at 95 °C and genotypes were analyzed using an ABI 3730xl DNA analyzer (Applied Biosystems, Carlsbad, California, USA). We scored genotypes with GeneMapper v. 4.0 software (Applied Biosystems, Carlsbad, California, USA) and individually verified them by visual inspection. To identify possible allelic dropout, we performed all microsatellite amplifications at least four times using the multi-tube approach (Taberlet et al. 1996). Allelic dropout and PCR success was quantified per locus, based upon sample type (scat vs. blood/tissue vs. historic specimen) using the program GIMLET (Valière 2002) and manual inspection. Consensus genotypes were defined for each sample by comparing results from a consensus genotype inference method using program GIMLET (Valière 2002), as well as manual inspection. Samples that did not produce reliable consensus genotypes for at least 10 loci were excluded from further analyses.

The 2014 scat survey samples were analyzed at the Laboratory for Ecological, Evolutionary and Conservation Genetics (University of Idaho, Moscow, Idaho) using protocols outlined by Davidson et al. (2014). Protocols were similar to those outlined above, apart from the main difference of using 10 microsatellite loci from the domestic cat (*Felis catus*) for individual identification (Menotti-Raymond et al. 1999, 2005), as opposed to the Kurushima et al. (2006) microsatellites.

*Statistical Analysis.*— We analyzed consensus genotypes in the R package allelematch (Galpern 2015) to determine the individual identities of cougars represented

in the samples. Noninvasively collected genetic data can be especially prone to genotyping errors and missing data (Waits and Paetkau 2005); allelematch was written specifically for analyzing this type of data for the purpose of identifying unique individuals in a population of unknown size (Galpern et al. 2012). Allelematch accommodates these imperfect datasets by calculating a pairwise similarity score between genotypes, and then identifying an optimal parameter of acceptance for imperfect allele matches (or a “mismatch tolerance”; see Fig. 3.9). Allelematch then produces an estimate of the number of unique genotypes represented in the sample. See Galpern et al. (2012) for details on the framework and application of the software.

*Density estimation.*— The resulting capture histories were comprised of one sampling occasion. Consequently, we were limited to single-occasion approaches such as the abundance estimator CAPWIRE (Miller et al. 2005) or certain SECR models. CAPWIRE was designed specifically for genetic sampling under the concept that this type of sampling is often “approximately done with replacement” (Miller et al. 2005), and usually performed on a single sampling occasion. CAPWIRE may be ideal for genetic sampling techniques such as ours, in which 1) there is only one sample occasion, 2) sampling is completely passive, and modeling for trap response behavior is not applicable, and 3) the sampled population is relatively small. Small population size is significant in that detections may be relatively rare, and therefore more informatively valuable. CAPWIRE retains all capture data, whereas traditional CMR techniques often must pool captures of an individual into a finite number of occasions, potentially squandering information. We note that Bromaghin (2007) critiqued CAPWIRE for utilizing a mathematically invalid likelihood function. However, this may be a minor



issue, as repairing the likelihood function does not alter CAPWIRE's abundance estimation (Bromaghin 2007). Furthermore, a genetic mark-recapture study by Davidson et al. (2014) used CAPWIRE to produce abundance estimates of cougars that were comparable to more traditional CMR methods. We ran CAPWIRE as implemented in the R package *capwire* (Pennell et al. 2013) using two models: the "equal catchability model" (ECM) and the "two innate rates model" (TIRM), and evaluated them using a likelihood-ratio test. The ECM and TIRM are analogous to homogenous and heterogeneous probabilities of detection in the traditional CMR framework. We calculated 95% confidence intervals for the model results using a parametric bootstrap, as implemented in the CAPWIRE package. To convert CAPWIRE abundance estimates into density, we delineated an effective trapping area around the sampling transects. The effective trapping area for the winter tracking transects was identical to the area divisor (Chapter 2). The effective trapping area for the detection dog survey was calculated identically to the method for the remote camera survey, using the geographic centers of scat transects as the buffering points.

We used the R package *secr* (Efford 2015) to estimate population density directly. The *secr* package allowed for single occasion detection histories, as well as the use of transect lines as the detector, whereas SPACECAP was limited to point-based trap arrays. Package *secr* uses spatially explicit capture-recapture models analogous to SPACECAP, but instead of a Bayesian framework, *secr* implements maximum likelihood to determine the spatial detection model. Parameters estimated were analogous to SPACECAP, but *secr* uses the notation  $g_0$  instead of  $\lambda_0$ . We inputted the trap transects as a single-occasion detection history, and a spatial mask layer of potential home range center points, spaced

at 5 km, analogous to the SPACECAP methods outlined above. We ran the null secr models, as well as models that incorporated a spatially varied density estimate that attempted to fit a gradient in cougar density along latitude or longitude (as was observed between the Buffalo Valley and Gros Ventre sampling areas). We also ran group models based on sex class, when that information was available. Behavioral models were not applicable due to our use of a single occasion. Models were evaluated using the corrected Akaike's Information Criterion (AIC<sub>c</sub>; Burnham and Anderson 2002).

*Demographic correction factor.*— Since genetic surveys are not able to distinguish age classes, our genetic surveys essentially used a different sampling frame than that for the photographic and reference methods. To address this issue in the context of comparing photographic and genetic sampling results, we estimated a correction factor based on likely number of dependent juveniles in the population. Based on average male to female ratios and number of dependent young observed in several cougar populations (Quigley and Hornocker 2010), we used a male : female : juvenile age class ratio of 1.0 : 2.5 : 2.5 to estimate that the total population (as estimated by the genetic sampling efforts) was 1.7 times greater than the adult population (as estimated by photographic and reference methods).

## RESULTS

### Photographic Sampling

*Blood lure detections.*— We were logistically constrained by the size of and number of stations in the camera trap array, and camera stations were not all active for the exact same time period or number of days. For the respective years, the average

number of days sampled per blood-lure camera station were 73.5 ( $\pm$  3.9 SD) and 79.4 ( $\pm$  8.1 SD), and the total number of sampling days were 3,160 and 3,414. The mean total length of the sampling windows (calculated from the first camera activation to last deactivation) was 100.0 days ( $\pm$  5.0 SD,  $n = 2$ ). We recorded 17 and 16 cougar photo-events in 2012 and 2013, respectively (Table 3.1). The average detection rate for the blood-lure stations was 0.15 detections per 30 sampling days. There was an average of 17.03 ( $\pm$  9.67 SD) photos per detection event. Based on physical characteristics (including artificial tags) and spatial/temporal distances between detections, we identified 5 and 7 unique individuals, respectively. Based on detections per sampling day, detections were significantly more likely to occur in the Gros Ventre ( $n = 25$ ) than the Buffalo Valley ( $n = 7$ ; two sample test for equality of proportions:  $\chi^2 = 7.74$ ,  $df = 1$ ,  $P < 0.01$ ). The mean number of recaptures per cougar was 3.0 ( $\pm$  2.3 SD) for 2012, and 2.3 ( $\pm$  1.1 SD) for 2013.

*Trail cameras.*— The trail camera arrays recorded 6 and 9 additional cougar detection events for 2012 and 2013, respectively (Table 3.1). For the respective years, the average number of days sampled per camera station were 34.9 ( $\pm$  9.7 SD) and 52.6 ( $\pm$  9.2 SD), and the total number of sampling days were 349 and 579. The average detection rate was 0.52 detections per 30 days, significantly higher than that of the blood cameras (two sample test for equality of proportions:  $\chi^2 = 13.90$ ,  $df = 1$ ,  $P < 0.001$ ). There was an average of 5.6 ( $\pm$  6.3 SD) photos per detection event, significantly lower than that for the blood cameras (Welch two-sample test;  $P < 0.001$ ).

*Conventional CMR.*— Due to low numbers of detections and unique individuals, we were limited to relatively simple closed-population CMR models. We applied the null

model ( $M_0$ ), behavioral model ( $M_b$ ), and the heterogeneity model ( $M_h$ ). Likely due to the low numbers of detections and of unique individuals, the models essentially produced the minimum abundances: all models for 2012 produced abundance estimates of 5 cougars, and all models for 2013 produced abundance estimates of 7 cougars. Confidence intervals were close to zero for all models except for the behavioral model in 2012; this model found a relatively strong “trap happy” response with low initial capture probability, thus increasing the abundance estimate. However, the behavioral model for 2013 indicated a “trap shyness” response (Table 3.2). The average female home range size during camera trapping months was  $190.0 \text{ km}^2$  ( $\pm 109.3 \text{ SD}$ ,  $n = 15$ ). The effective trapping area was thus calculated with a buffering distance equal to the radius of this area: 7,769 m. This resulted in effective trapping area sizes of  $1,215 \text{ km}^2$ ,  $1,474 \text{ km}^2$ , and  $2,333 \text{ km}^2$  for the Buffalo Valley, Gros Ventre, and combined areas, respectively. The abundance estimates calculated in program MARK converted to density estimates of 0.21 cougars per  $100 \text{ km}^2$  for 2012 and 0.30 cougars per  $100 \text{ km}^2$  for 2013. We also note here that the detector generated  $\frac{1}{2}$  MMDM (based on our assessment of individual identity) was 4,825 m in 2012 and 2,519 m in 2013. The  $\frac{1}{2}$  MMDM metric was significantly lower than the telemetry derived buffer amount, consistent with findings for jaguars by Soisalo and Cavalcanti (2006). Due to poor model performance, we limited the density estimate to the combined area and did not attempt to subdivide abundance estimates for the Buffalo Valley or Gros Ventre areas.

*Spatially explicit model.*— Based on the Geweke diagnostic, models that incorporated a behavioral response performed poorly and were discarded. For behaviorally null models, SPACECAP produced posterior mean densities of 0.36 (95%

HPD = 0.18 – 0.64) and 0.84 (95% HPD = 0.40 – 1.40) cougars per 100 km<sup>2</sup> for 2012 and 2013, respectively (Table 3.3). Models restricted to the Gros Ventre were not consistent in performance, and models restricted to the Buffalo Valley were not run due to low numbers of detections. Density estimates were generally in agreement with home range centers (Fig. 3.7) as calculated in SPACECAP.

*Detections of radio-tagged cougars.*— In the 2012 season, 7 of the 23 total photo detections (29.2%) were detections of radio-collared cougars. In 2013, 5 of the 25 total photo detections (20.0%) were radio-collared. There were 8 radio-collared individuals present on the remote camera array in 2012. Based on our assessment of individual identity, 5 out of the 8 individuals photographed were not collared (62.5%). There were 7 radio-collared individuals on the remote camera array in 2013. Of the 12 photo-detected individuals, 8 were uncollared (66.7%). The two-sample Lincoln-Petersen estimator produced abundance estimates of 19.25 (95%CI = 9.39 – 29.11), with photo detection probability ( $p_2$ ) of 0.42 (given  $p_1$  of 0.42), and 19.80 (95%CI = 11.80 – 27.80), with photo detection probability of 0.61 (given  $p_1$  of 0.35), for the respective years.

We used a generalized linear mixed-effect model (GLMM) with a Poisson distribution to examine if the density of camera stations within an individual's home range was related to the count of that individual's detections. We used the GLMM framework in order to add individual ID as a random effect and account for the variability between and autocorrelation within the individuals' location sets. We found a negative but insignificant correlation between number of detections and detectors per km<sup>2</sup> ( $\beta$  = -15.31, SE = 14.2,  $P$  = 0.28).

*Reliability of identifying individual cougars in photographs.*— We subsampled 15 events (resulting in 105 combinations of event pairs) from the 2013 remote camera survey to distribute to independent participants. We collected results from 7 participants. Each set of results included the list of 105 event pair combinations with participants' scoring of each pairing as "same cougar" or "different cougars". The number of unique individuals identified by participants ranged from 4 to 13. The mean number of identified individuals was 9 ( $\pm 3.5$  SD). Using the R package irr (Gamer et al. 2014), we found a 46.7% simple agreement between participants. Using Fleiss's kappa, we found a kappa value of 0.183 ( $P = 0$ ). Although interpretation of kappa values is somewhat subjective (Gwet 2010), this value would usually be categorized as "slight" (Landis and Koch 1977) or "poor" agreement (Fleiss et al. 1981). Of the event pairings with full participant agreement, 100% were for differentiated individuals; there were no cases of full agreement when ascribing the paired events to the same individual. Out of the 105 event pairings, there were only 6 with >50% of participants ascribing them as "same". The mean distance between pairings with >50% of participants differentiating individuals was 18.1 km ( $\pm 8.4$  km SD,  $n = 99$ ), and the mean distance between pairings with >50% of participants ascribing "same" status was 1.3 km ( $\pm 3.1$  km SD,  $n = 6$ ). Of the 6 pairings with >50% "same" agreement, 4 were from event pairs occurring at the same camera station. Our simple agreement level of 46.7% was much lower than a similarly derived agreement level of 79.3% reported by Kelly et al. (2008). Of note, Kelly et al. (2008) used approximately three times as many detection events in their survey, despite a similar average number of identified individual cougars. Interestingly, we used 7 independent investigators, and Kelly et al. (2008) used 3 independent teams. This is notable because

we found that percent agreement decreased as the number of investigators increased: we reran our calculations for percent agreement using all possible combinations and subsets of the participant pool. The mean percent agreement for any subset of three investigators increased to 71.4% ( $\pm 13.5$  SD) and ranged from 54.3% - 91.4% (Fig. 3.8).

To examine our hypothesis that a greater number of photos per event would aid in identification, we performed a generalized linear model with a Poisson distribution to examine the level of agreement for an event matching as a function of the number of photos used in the matching. We found no significant correlation ( $\beta = -0.009$ ,  $SE = 0.008$ ,  $P = 0.24$ ). We also used a spatial-temporal measure of the minimum speed required for an individual cougar to be present at both events in a matching. We used the natural log transformation to normalize the value and found a significant negative correlation ( $\beta = -0.21$ ,  $SE = 0.03$ ,  $P < 0.001$ ) between higher minimum speed and count of “same” designations indicating that distance and time were likely important in participant’s assessments, although it is uncertain if participants made decisions mainly based on spatial-temporal data, or if participant’s decisions were correct, and supported by the spatial-temporal data.

### **Genetic Sampling**

*Winter tracking transects.*— We surveyed 454 km of transects in the 2012 season, and 824 km in the 2013 season, totaling 1,276 km. The mean survey length was 102.0 days ( $\pm 17.0$  SD,  $n = 2$ ). The mean sampling window was 2.21 days of cougar travel time after snowfall per transect ( $\pm 1.04$  SD). Between 1 and 8 observers participated in transects per snowfall event ( $n = 13$ ,  $\bar{x} = 3.6 \pm 1.8$  SD). We encountered 11 and 8 suspected cougar tracks for the two seasons, respectively. Over the course of the study,

tracks were encountered on average once per 67.26 km transected, and once per 0.68 days of sampling. Based on sampling effort, tracks were more likely to be encountered in the Gros Ventre than the Buffalo Valley area ( $n = 5$  in Buffalo Valley;  $n = 14$  in Gros Ventre; two sample test for equality of proportions:  $\chi^2 = 4.71$ ,  $df = 1$ ,  $P < 0.05$ ). We collected usable hair samples from 9 of these encounters. Using mitochondrial analysis, 6 samples were identified as cougar hair. The other three were identified as Canid ( $n = 2$ ) or “unknown species” ( $n = 1$ ). Only 2 of the samples were amplified to the individual level, negating any subsequent mark-recapture analysis.

*Scat detection dogs.*— We completed 20 transects across the study area both in 2013 and 2014. The mean survey length was 26.0 days ( $\pm 1.4$  SD,  $n = 2$ ), although, due to the uncertainty of scat DNA degradation, this should not be interpreted as the sampling window. Based on handheld-GPS data, handlers transected approximately 199 km per year (76.5 km in the Buffalo Valley, 106.3 km in the Gros Ventre). The mean transect length was 9,928 m ( $\pm 1,633.7$  SD). A total of 219 scat samples were collected: 129 in 2013 and 90 in 2014. The mean number of scats collected per transect was 5.4 ( $\pm 5.2$  SD), with 3.4 ( $\pm 2.1$  SD) in the Buffalo Valley and 6.8 ( $\pm 6.2$  SD) in the Gros Ventre. Of these, 78.1% were determined to be cougar scat based on mDNA analysis. The remaining scat samples were either non-target species or were unable to be verified due to poor quality of sample (86.4% success rate for field detection when excluding those samples that failed to yield a species identification). Non-target species were generally identified as canid (red fox, coyote, grey wolf, or unknown canid). Two samples were identified as ursid, one as cervid, and 15 samples were identified as unknown, non-target species. After discarding non-target scats via mDNA analysis, the number of cougar scats



collected for each year differed by only 3.6% ( $n = 87$  in 2013;  $n = 84$  in 2014). This may have indicated an improvement in detection ability between the two years: of the samples that provided an mtDNA-based species identification, 29.9% were non-target in 2013, and 1.2% were non-target in 2014. However, since two different labs and lab analyses were used in the two years, this comparison is not necessarily appropriate. Based on scats detected per length of transect, there were significantly more cougar scats detected in the Gros Ventre than the Buffalo Valley ( $n = 40$  in Buffalo Valley;  $n = 131$  in Gros Ventre; two sample test for equality of proportions:  $\chi^2 = 17.223$ ,  $df = 1$ ,  $P < 0.001$ ). Of these verified cougar scats, 83 were genotyped (48.5% success rate for microsatellite analysis of confirmed cougar scat) and analyzed with the R package *allelematch*. In 2013, *allelematch* determined an optimum mismatch tolerance parameter of 6 (Fig. 3.9). Using this parameter, *allelematch* identified 28 unique genotypes within 50 of the genotyped scats. Two genotypes were discarded due to missing alleles which created high ambiguity of identity. Of the 28 unique genotypes, 22 were in the Gros Ventre (78.6%), 5 were in the Buffalo Valley (17.9%), and 1 was detected in both areas (3.6%). In 2014, *allelematch* determined an optimum mismatch tolerance parameter of 4, and identified 17 unique genotypes within the 32 genotyped scats. Of the 17 unique genotypes, 9 were in the Gros Ventre (52.9%) and 8 were in the Buffalo Valley (47.1%). The relatively similar number of individuals detected between the Gros Ventre and Buffalo Valley in 2014 was surprising. However, this was likely due to the uneven PCR success rate between the two areas: the Gros Ventre samples were 28.1% successful in individual genetic identification, and Buffalo Valley samples were 50.0% successful. As a comparison, these values in 2013 were 42.3% and 32.0%, respectively.

*CAPWIRE models.*— The CAPWIRE equal catchability model (ECM) produced a maximum likelihood abundance estimate of 38 (95% CI = 29 – 50) in 2013, and 27 (95% CI = 19 – 38) in 2014. The two-innate rates model (TIRM) produced abundance estimate of 55 (95% CI = 42 – 89) in 2013 and 48 (95% 34 - 98) in 2014. The model fit comparison tests produced high values for the likelihood ratio: in 2013 the likelihood ratio was 12.94 ( $P < 0.05$ ), and in 2014 the likelihood ratio was 13.98 ( $P = 0$ ), strongly suggesting that we could reject the null equal catchability model. In order to calculate density, we buffered transects from their geographic centers by 7,769 m (similarly to the remote cameras) to delineate the effective trapping areas. The Buffalo Valley, Gros Ventre, and combined areas were 648 km<sup>2</sup>, 816 km<sup>2</sup>, and 1,401 km<sup>2</sup>, respectively. The resulting TIRM density estimates for the Buffalo Valley, Gros Ventre, and combined areas, respectively, were 2.78, 5.51, and 3.93 cougars per 100 km<sup>2</sup> in 2013, and 2.78, 4.04, and 3.43 cougars per 100 km<sup>2</sup> in 2014 (Table 3.4).

*Spatially explicit models.*— Based on AIC<sub>c</sub> ranking, the top SECR model in 2013 incorporated a density gradient along north-south and east-west lines, reflecting the different cougar densities in the Buffalo Valley and Gros Ventre areas (Table 3.5). For the Gros Ventre area, the top 2013 model was the null model. Due to lack of re-detections in the Buffalo Valley in 2013, we could not run any SECR models. In 2014, the top model for the Gros Ventre, Buffalo Valley, and combined areas was the null model (Table 3.6). In 2014 we also ran group models incorporating the genetically determined sex of the individuals. Genetic classification of sex was 10.4% unsuccessful, and detections with unknown sex had to be excluded from the group models. Due to small sample size, we discarded models with greater than 6 parameters; these models

performed poorly, and failed to produce AIC<sub>c</sub> scores. The null models were the highest ranked for the Gros Ventre and Buffalo Valley. For the combined areas, there was approximately equal evidence for a group effect for  $g_0$  (Table 3.7) indicating a higher probability of detection for males, which is possible given that transect routes generally followed ridgelines and travel routes where cougar scrape sites were common, and where males may be more likely to deposit scat (Harmsen et al. 2010). We used model averaging, as implemented in Package *sear*, to determine results for the combined area (Table 3.8).

*Detections of radio-tagged cougars.*— Due to differing lab protocols, we were only able to cross-reference genetic samples collected directly from radio-collared animals to the scat data collected in 2013. Of the 28 unique genotypes detected in the scat samples from 2013, 4 were identified as previously captured and radio-collared individuals. We determined there were 7 radio-collared individuals on the transect array during 2013. We used a generalized linear mixed-effect model (GLMM) with a Poisson distribution to examine if the density of scat detection transects within an individual's home range was related to the number of times an individual was detected. We found a positive but nonsignificant correlation between the number of detections and detectors per km<sup>2</sup> ( $\beta = 0.531$ ,  $SE = 0.486$ ,  $P = 0.275$ ).

### **Comparisons with Reference Estimates**

Expressed as a density estimate of cougars per 100 km<sup>2</sup>, the mean of the telemetry-derived density estimates for 2011 – 2013 was 1.07 in the Gros Ventre area ( $n = 3$ ,  $\pm 0.15$  SD), 0.26 in the Buffalo Valley area ( $n = 3$ ,  $SD = 0.07$ ), and 0.82 for the combined areas ( $n = 3$ ,  $\pm 0.10$  SD) (Chapter 2). After adjusting to include the non-adult

residents that were likely in the population and detected in genetic sampling, the respective estimates were 1.82 ( $n = 3, \pm 0.26$  SD), 0.45 ( $n = 3, \pm 0.12$  SD), and 1.40 ( $n = 3, \pm 0.16$  SD). Density estimates from the noninvasive techniques varied spatially and annually (Table 3.9) with some in agreement to density estimates derived from the radio-collared sample of cougars (Fig. 3.10).

Our survey of independent investigators (see above) suggested that our photographic detection histories were likely unreliable, due to inability to accurately assign individual identification to cougars. For the moment we ignore this caveat, and report the following comparisons under the assumption that our photographic tagging process was accurate. Our conventional CMR (MARK) based analysis of photographic captures produced results that were on average 68.3% lower than the reference estimate. Since our reference estimate included a small number of uncollared individuals for whom we were not 100% certain of residency (see Chapter 2), it was not categorically a minimum count. Nonetheless, it remains unlikely that the true density was lower than this reference estimate. The SECR-based models using SPACECAP produced more plausible results, likely in part due to our inclusion of trail camera photos in the encounter histories which increased the number of detections by an average of 45.8% per year. Promisingly, the 2013 SPACECAP estimate ( $D = 1.1$ ) was less than 2% different than the reference estimate ( $D = 1.07$ ). However, SPACECAP results had relatively high variance between the two seasons (relative SD = 56.5%), and, despite the greater number of detections, there were still issues of low sample size. The number of independent MCMC chains modeled (a measure of effective sample size for each model parameter) were especially problematic for  $\sigma$ , likely due to the low number of multi-detector recaptures (see Table

3.3). Both remote camera surveys coincided with telemetry-based surveys (2012 and 2013). We overlaid concurring annual home ranges of GPS-collared cougars on the pixel density maps produced by SPACECAP (Fig. 3.7). Home ranges were delineated by kernel density estimation, using the plugin bandwidth (Chapter 2).

Due to poor collection rates and genotyping success, the winter tracking transects did not provide density estimates with which to compare to the reference estimate. For the genetic sampling using scat detection dog surveys, the SECR-based density estimates were 71.8% greater than the adjusted telemetry-based reference estimates. The CAPWIRE estimates were on average 162.9% greater. Of note, the CAPWIRE equal catchability model (ECM) produced estimates closer to those for the reference estimate. However, based on the likelihood ratio test, the two innate rates model (TIRM) was more likely. Indeed, the TIRM was also more biologically appropriate given the high probability that a subset of the population included dependent young with lower innate capture probabilities than adults. Conversely, the AIC<sub>c</sub> scores as implemented in Package secr favored models that generally did not incorporate heterogeneous mixtures for any of the parameters (including capture probability), despite their biological plausibility.

### **Cost Comparison**

Estimated costs for the noninvasive surveys varied widely (Table 3.10). Some costs had to be estimated due to our use of volunteer support, as well as equipment and lab analysis that was donated in-kind. Outside of fuel costs, we did not account for the costs of trucks, snowmobiles, or ATVs. Remote camera surveys and winter tracking transects were intensive in their vehicle requirements, generally needing multiple vehicles per day of effort. The detection dog team provided its own vehicle, which was

accounted for in the personnel cost. Also, we did not include time spent on data analysis; this is especially relevant to the remote camera surveys, for which considerable time was spent in the process of sorting photographs and individually identifying cougars.

As a point of interest, we also report an estimate of the telemetry based “cost per enumeration” (i.e., the physical capture, tagging and radio-collaring as described in Chapter 2). We added the amount spent on GPS collars, collar refurbishments, houndsman services, immobilization drugs, and capture equipment over the course of 18 captures (including recaptures for collar replacement) that occurred between 2011 and 2014. Divided between the 14 individuals tracked, this results in a cost per enumeration of \$5,426. This amount does not include general overhead costs: since captures were performed as part of a large scale ecological study on cougars, we were unable to parse out the costs of personnel, vehicles, and gas used in capture efforts from those of the wider study, and this estimate should be considered a minimum. Furthermore, we stress that it is not necessarily appropriate to directly compare this amount to the cost per noninvasive detection described above.

## **DISCUSSION**

Using our techniques and analyses, scat detection dogs were more efficient in generating detections of cougars than the other methods attempted. Based on our survey of independent investigators’ agreement in identifying photo-captured cougars, scat detection dogs were also less prone to error. More research is needed to determine the effective sampling window of scat detection dogs, although, based on work by Lonsinger et al. (2015), the sampling window of our scat detection dog survey was unlikely greater

than that for the remote camera or winter tracking surveys. Based on the detections of collared individuals, the scat detection surveys were slightly more effective: the 2013 scat survey detected 4 out of the 7 collared individuals (57.1%) present on the trapping array. The remote cameras detected 3 out of 8 and 4 out of 7 for the respective years, for an average of 47.3%. Based on our regression analyses of detectors per individual home range, there was no significant relationship between the density of detectors (either remote camera or scat transect) in a home range and the probability of being detected. Possibly a more important factor for remote camera detections was the placement of camera stations as opposed to the number of stations (i.e., one well-placed camera along a travel route will outperform several camera stations placed in less traveled locations). This highlights the difficulties in point-trapping animals with large home ranges over heterogeneous terrain, for which the detection probability of individual traps will vary significantly. Our analysis of density of scat transects per home range also failed to show any significant association. However, the relationship was nonetheless positive, and the model was limited to a single season.

For both remote cameras and scat detection dogs, SECR-based analyses produced results more comparable to the reference estimate than non-SECR analyses. Presumably, SECR has better applicability to cougar populations because conventional CMR assumptions for cougars are particularly problematic, such as closure issues related to large home ranges extending beyond the edge of the trapping array. Large home ranges were also problematic for determining the trapping buffer for non-SECR methods. We used GPS telemetry data to determine the buffer length, whereas a naively determined buffer width would have used the  $\frac{1}{2}$  MMDM metric determined from trap locations. The

mean remote camera generated estimate was 52.7% less than the telemetry-derived home range radius; the estimate from the scat detection dog transects was 51.5% less.

Alternative field techniques for the surveys may have changed their resulting estimates to some degree. For example, problems for the winter tracking transects included both very low detection rates and low success in genotyping samples. Sampling rate issues were possibly due to having too strict of protocols for the timing of transects: weather conditions were rarely ideal, and often did not provide a distinct sampling window with 2-3 days of calm tracking conditions. In addition, winter travel restrictions were in effect in certain parts of the study area, thereby limiting access to backtrack and collect hair samples. A subset of samples was identified as a canid species using mDNA analysis. All investigators were well trained in identifying cougar tracks; therefore this was most likely due to cross contamination at bedsites or in snow tracks as opposed to misidentification of tracks. Poor genotyping success was likely due to insufficient hair quantity, reinforcing statements by Kendall and McKelvey (2008) and genotyping success rates reported by Sawaya et al. (2011) and Russell et al. (2012). Potentially, the low rates of genotyping success accompanying shed cougar hair are not appropriate to relatively low density cougar populations such as ours. Based on our research, we would recommend that winter transects be performed with greater than our average of 3.5 observers per sampling stint. Observers should also collect a greater amount of hair (our samples were generally 4 – 5 hairs per sample), or increase tracking length to collect a more viable scat sample. Regardless, the scat detection dog surveys were 127.4 times more fruitful than the winter track transects in terms of detections per person-day of effort. This is in part due to the poor genotyping success of the collected hair samples:



winter transects only yielded a track-detection-to-individual-identity ratio of 11%. Given a hypothetical scenario of 100% genotyping success with all collected samples, the scat detection dog team would have still generated 33.3 times as many genotypes per person-day as the winter transects.

For the remote camera surveys, the most critical finding was that our photographic survey estimates were unreliable, mainly due to the inability to reliably identify individual cougars. Conceivably improved photo quality, either using improved camera technology or field techniques, would alleviate this problem. This issue has important implications regarding other remote camera density estimates for cougars that rely on photographic identification of individuals (e.g., Kelly et al. 2008, Negroes et al. 2010, Urios et al. 2010). Conceivably, these studies' use of conventional camera station setups (one or two cameras placed along high use trails without a lure to prolong detection events and increase photo quantity) resulted in more accurate individual identification. However, we found no correlation between investigator agreement and number of photos within a detection event. Kelly et al. (2008) also found no significant relationship between photo quality and ability of investigators to assign identification. Nevertheless, given the success of camera trapping studies on other felids (e.g., Karanth 1995, Trolle and Kéry 2003, Soisalo and Cavalcanti 2006), further research on the field techniques of photo-trapping cougars is still warranted. Disregarding the issue of identifiability, we found a 71% higher rate of detection for the trail sites over the blood lure stations, suggesting the trail camera setup was a more efficient method for generating detections. This discrepancy was possibly due in part to the blood stations being restricted from human use trails, which often overlapped topographic features where

cougars were more likely to be detected (e.g., ridgelines, drainage bottoms), supporting our impression that well-placed passive detectors may be more effective than less ideally placed baited detectors. Trail sites were also less costly; the blood lure camera stations had a higher maintenance cost than the trail cameras due to the need to regularly replace the blood lure. Furthermore, due to the possibility of bear encounters, safety protocols prohibited visits to blood lure stations with fewer than two technicians, whereas trail sites could be visited solo. Regardless, the scat detection surveys produced 730% more detections per unit of survey length than the trail cameras and at a lower cost. We did not calculate the trail cameras' detections per person day of effort. The blood-lure sites had a 261% greater number of photos taken per detection event over the trail sites, supporting our hypothesis that cougars would spend more time investigating the site because of the lure. However, we were wrong in our hypothesis that a greater number of photos would increase an observers' ability to identify unique individuals. There was a promising spatial correlation between the SPACECAP produced estimates of density and the concurrent GPS-collar derived home ranges. Although the reliability of our density estimates was uncertain, this spatial correlation suggested some promise assuming resolutions to the issues outlined above.

Our survey methods were not necessarily comparable to work by Davidson et al. (2014), due to that study's greater survey effort, smaller sampling area, and use of multiple sampling occasions of scat dog transects allowing for conventional CMR using program MARK. However, it is worth noting that Davidson et al. (2014) reported a similar scat collection rate, number of unique genotypes, and genotyping success. Of note, Davidson et al. (2014) reported some of the largest capture probabilities published

for felids (0.25-0.99), whereas our SECR based capture probabilities ranged from 0.03-0.05 (Table 3.6). Our sampling transects were sparse relative to the Davidson et al. (2014) study; however, the average spacing between nearest transect neighbors (calculated from transect center points) was 4,028 m and unlikely to only cover a single cougar home range. The scat detection dog encounter histories nevertheless had a high number of singletons (i.e., unique genotypes that were only encountered once): 60.7% and 70.6% of individual genotypes were detected only once in 2013 and 2014, respectively. These singletons could be explained by low sampling effort, inherently low detection probabilities for some portion of the population, or both. An increase in sampling effort would very likely increase our estimated capture probabilities, and potentially reduce singleton detections. However, another explanation is that the population during the sample included a high number of transient cougars. In this scenario, there would be erroneously inflated population estimates to some degree, due to transient individuals' inherently low detection probability, depending on the length of time spent on the transect array. To examine this, we reran the top SECR models for the combined areas, excluding the singleton detections. The 2013 model estimated a density of 0.81 cougars/100 km<sup>2</sup> (95% CI = 0.32 – 2.06); the 2014 model estimated 0.50 cougars/100 km<sup>2</sup> (95% CI = 0.19 – 1.30). These estimates were low compared to the reference estimate of 1.40 cougars/100 km<sup>2</sup>. Although detection count was probably related to residency status, the singletons in our sample likely included residents as well as transients, given the relatively low recapture counts: the mean detection count per individual was 1.78 (n = 45,  $\pm$  1.43 SD), and the mean detection count for non-singleton individuals was 3.33 (n = 15,  $\pm$  1.59 SD). The inclusion of transients in the sample is

essentially an issue of population closure; despite SECR models' relaxed assumptions of closure, truly transient individuals (as opposed to temporary immigrants or emigrants; see Kendall et al. (1997); Gardner et al. (2009)) are problematic given there would not be any home range to be modeled. Survey timing may help with this issue. Ruth et al. (2011) found >90% of dispersing subadult cougars in the Greater Yellowstone Ecosystem migrated between April and September. Our surveys were performed in the late summer months; depending on the temporal sampling window, we likely sampled from this migratory period. This issue reiterates the issue of uncertainties in the temporal sampling window for cougar scat surveys given different environmental conditions that likely affect scat detectability and DNA integrity at various rates (Lonsinger et al. 2015). We recommend timing detection dog transects after spring snowmelt, but before the likelihood of detecting transient individuals increases. An ideal collection time may be further refined given more information on the DNA degradation rate for cougar scat samples.

Many carnivore species have undergone significant contractions in their historic distributions due to habitat loss, habitat fragmentation, or direct persecution by humans (Laliberte and Ripple 2004), resulting in a call for increased effort in carnivore conservation (Gittleman et al. 2001). Reliable population estimates are vital for the implementation and evaluation of any conservation effort, and noninvasive methods to determine these estimates may provide researchers the ability to measure population size at relatively low cost. In this thesis, we examined a current issue related specifically to the management and conservation of cougars: the need for a low cost alternative to the costly "gold standard" method of capturing and radio-collaring all individuals in a

population to determine its size. We examined several noninvasive techniques which have been used to survey cougar populations, but not necessarily in conjunction with other noninvasive methods or a comparative “gold standard” estimate. Based on our “gold standard” estimate (Chapter 2), the remote camera surveys and scat dog surveys both produced plausible density estimates. However, financial cost being a chief motivation behind the need for accurate noninvasive survey methods, we emphasize that our scat detection dog surveys were an order of magnitude less expensive than the other types of surveys (in terms of cost per detection). Future research should address the timing, temporal sampling window, and statistical power of this method. We also determined that photographic detections of cougars are likely unsuitable for CMR analyses, demonstrating a critical difference between survey options for cougars and other conspicuously pelaged felids such as tigers, leopards and jaguars. However, some researchers may prefer to use remote cameras, for reasons such as being able to detect multiple species without the need for scent training a dog to specific species. Therefore, future research is warranted provided that consideration is given to the issue of identifiability, as well as the method’s relatively lower detection rate.

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Table 3.1. Comparison of detection and photo rates for blood lure camera stations and conventional trail cameras for sampling cougars noninvasively, northwestern Wyoming, 2012-2013.

| Camera station design | Year | Number of camera stations | Number of detections | Total sampling days | Detection rate per 30 days | Mean photos per event | ± SD photos per event |
|-----------------------|------|---------------------------|----------------------|---------------------|----------------------------|-----------------------|-----------------------|
| Blood lure sites      | 2012 | 43                        | 17                   | 3160                | 0.149                      | 16.8                  | 10.7                  |
|                       | 2013 | 43                        | 16                   | 3414                | 0.141                      | 27.3                  | 8.8                   |
| Trail sites           | 2012 | 10                        | 6                    | 348                 | 0.517                      | 8.6                   | 9.0                   |
|                       | 2013 | 12                        | 9*                   | 579                 | 0.466                      | 3.6                   | 2.7                   |

\*one detection event comprised 2 kittens with an adult; the kittens were not included

in the total

Table 3.2. Parameter estimates for cougars sampled noninvasively in northwestern Wyoming, as determined from program MARK.

Density was calculated using the effective trapping buffer determined from mean home range size.

| Year | Model          | Parameter | Estimate | SE   | 95%Lower | 95%Upper | Density | Density range |
|------|----------------|-----------|----------|------|----------|----------|---------|---------------|
|      |                |           |          |      | CI       | CI       |         |               |
| 2012 | M <sub>0</sub> | N         | 5.00     | 0.00 | 5.00     | 5.00     | 0.21    | (0.21-0.21)   |
|      |                | p         | 0.33     | 0.07 | 0.20     | 0.48     | -       | -             |
|      | M <sub>b</sub> | N         | 5.88     | 3.49 | 5.03     | 28.62    | 0.25    | (0.22-1.23)   |
|      |                | p         | 0.17     | 0.18 | 0.02     | 0.71     | -       | -             |
|      |                | c         | 0.44     | 0.12 | 0.24     | 0.67     | -       | -             |
|      | M <sub>h</sub> | N         | 5.00     | 0.00 | 5.00     | 5.00     | 0.21    | (0.21-0.21)   |
|      |                | p         | 0.33     | 0.07 | 0.20     | 0.48     | -       | -             |
|      |                | $\pi$     | 0.50     | 0.00 | 0.50     | 0.50     | -       | -             |
| 2013 | M <sub>0</sub> | N         | 7.00     | 0.00 | 7.00     | 7.00     | 0.30    | (0.30-0.30)   |
|      |                | p         | 0.29     | 0.06 | 0.18     | 0.42     | -       | -             |
|      | M <sub>b</sub> | N         | 7.00     | 0.00 | 7.00     | 7.00     | 0.30    | (0.30-0.30)   |
|      |                | p         | 0.35     | 0.11 | 0.18     | 0.57     | -       | -             |
|      |                | c         | 0.25     | 0.07 | 0.14     | 0.41     | -       | -             |
|      | M <sub>h</sub> | N         | 7.00     | 0.00 | 7.00     | 7.00     | 0.30    | (0.30-0.30)   |
|      |                | p         | 0.29     | 0.06 | 0.18     | 0.42     | -       | -             |
|      |                | $\pi$     | 0.50     | 0.00 | 0.50     | 0.50     | -       | -             |

Table 3.3. Parameter estimates for a cougar population in northwestern Wyoming, as determined from remote camera surveys using spatially explicit models as implemented in SPACECAP.

| Year | Area             | Camera array       | Parameter   | Posterior mean | Geweke diagnostic | Effective sample size | Posterior SD | 95% Lower HPD level | 95% Upper HPD level |
|------|------------------|--------------------|-------------|----------------|-------------------|-----------------------|--------------|---------------------|---------------------|
| 2012 | Total Study Area | Blood lure cameras | $\sigma$    | 6,058          | -0.33             | 455.3                 | 3,087        | 2,925               | 10,891              |
|      |                  |                    | $\lambda_0$ | 0.077          | 0.27              | 1,023.6               | 0.047        | 0.011               | 0.169               |
|      |                  |                    | $\psi$      | 0.238          | -0.73             | 2,617.1               | 0.115        | 0.049               | 0.462               |
|      |                  |                    | N           | 14.979         | -0.69             | 2,239.2               | 6.932        | 5.000               | 28.000              |
|      |                  |                    | D           | 0.331          | -                 | -                     | 0.153        | 0.110               | 0.618               |
|      |                  |                    | p           | 0.073          | -                 | -                     | 0.042        | 0.011               | 0.155               |
|      |                  | All cameras        | $\sigma$    | 10,254         | -0.43             | 512.4                 | 4,160        | 5,329               | 1,6391              |
|      |                  |                    | $\lambda_0$ | 0.032          | -0.54             | 1,731.8               | 0.015        | 0.007               | 0.062               |
|      |                  |                    | $\psi$      | 0.247          | 0.45              | 2,889.6               | 0.105        | 0.076               | 0.452               |
|      |                  |                    | N           | 16.278         | 0.31              | 2,367.3               | 6.482        | 8.000               | 29.000              |
|      |                  |                    | D           | 0.359          | -                 | -                     | 0.143        | 0.177               | 0.640               |
|      |                  |                    | p           | 0.031          | -                 | -                     | 0.015        | 0.007               | 0.060               |
|      | Gros Ventre      | Blood lure cameras | $\sigma$    | 258,423        | -1.18             | 6.0                   | 301,789      | 2,827               | 862,310             |
|      |                  |                    | $\lambda_0$ | 0.056          | 4.79              | 1,780.3               | 0.064        | 0.004               | 0.179               |
|      |                  |                    | $\psi$      | 0.141          | 3.33              | 3,635.1               | 0.094        | 0.021               | 0.335               |
|      |                  |                    | N           | 6.894          | 3.23              | 2,617.9               | 4.596        | 4.000               | 17.000              |
|      |                  |                    | D           | 0.210          | -                 | -                     | 0.140        | 0.122               | 0.518               |

|      |                  |                    |             |        |       |          |        |        |        |
|------|------------------|--------------------|-------------|--------|-------|----------|--------|--------|--------|
|      |                  |                    | p           | 0.053  | -     | -        | 0.056  | 0.004  | 0.164  |
|      |                  | All cameras        | $\sigma$    | 10,652 | 0.40  | 1,105.3  | 4,812  | 5,472  | 17,572 |
|      |                  |                    | $\lambda_0$ | 0.029  | -1.37 | 3,554.7  | 0.013  | 0.007  | 0.056  |
|      |                  |                    | $\psi$      | 0.221  | 0.62  | 10,619.3 | 0.085  | 0.078  | 0.391  |
|      |                  |                    | N           | 14.466 | 0.65  | 7,893.7  | 4.903  | 8.000  | 24.000 |
|      |                  |                    | D           | 0.441  | -     | -        | 0.149  | 0.244  | 0.732  |
|      |                  |                    | p           | 0.028  | -     | -        | 0.013  | 0.007  | 0.054  |
|      | Buffalo Valley   | Blood lure cameras | N/A         | N/A    | N/A   | N/A      | N/A    | N/A    | N/A    |
|      |                  | All cameras        | N/A         | N/A    | N/A   | N/A      | N/A    | N/A    | N/A    |
| 2013 | Total Study Area | Blood lure cameras | $\sigma$    | 5,924  | -0.84 | 653.3    | 1,953  | 3,198  | 9,646  |
|      |                  |                    | $\lambda_0$ | 0.062  | 1.10  | 1,220.6  | 0.031  | 0.013  | 0.124  |
|      |                  |                    | $\psi$      | 0.321  | -0.47 | 3,753.1  | 0.131  | 0.097  | 0.582  |
|      |                  |                    | N           | 21.195 | -0.46 | 2,893.0  | 8.212  | 8.000  | 37.000 |
|      |                  |                    | D           | 0.468  | -     | -        | 0.181  | 0.177  | 0.817  |
|      |                  |                    | p           | 0.060  | -     | -        | 0.029  | 0.013  | 0.117  |
|      |                  | All cameras        | $\sigma$    | 6,437  | -0.25 | 738.2    | 1692   | 3872   | 9,872  |
|      |                  |                    | $\lambda_0$ | 0.034  | -0.93 | 1,657.4  | 0.014  | 0.011  | 0.063  |
|      |                  |                    | $\psi$      | 0.526  | 0.37  | 2,291.4  | 0.170  | 0.222  | 0.875  |
|      |                  |                    | N           | 37.906 | 0.33  | 2,166.3  | 11.929 | 16.000 | 61.000 |



|                       |                          |             |           |       |          |         |           |           |
|-----------------------|--------------------------|-------------|-----------|-------|----------|---------|-----------|-----------|
|                       |                          | D           | 0.837     | -     | -        | 0.263   | 0.397     | 1.391     |
|                       |                          | p           | 0.034     | -     | -        | 0.014   | 0.011     | 0.061     |
| Gros<br>Ventre        | Blood<br>lure<br>cameras | $\sigma$    | 22,926    | -0.29 | 30.8     | 45,443  | 2,891     | 119,292   |
|                       |                          | $\lambda_0$ | 0.062     | -1.56 | 1,630.5  | 0.043   | 0.004     | 0.144     |
|                       |                          | $\psi$      | 0.224     | -1.05 | 2,611.2  | 0.137   | 0.031     | 0.498     |
|                       |                          | N           | 13.974    | -1.02 | 2,266.4  | 8.604   | 5.000     | 31.000    |
|                       |                          | D           | 0.426     | -     | -        | 0.262   | 0.152     | 0.945     |
|                       |                          | p           | 0.059     | -     | -        | 0.040   | 0.004     | 0.134     |
|                       | All<br>cameras           | $\sigma$    | 4,481,923 | -9.76 | 1,169.0  | 612,443 | 2,938,274 | 5,404,512 |
|                       |                          | $\lambda_0$ | 0.008     | 1.04  | 21,628.5 | 0.002   | 0.003     | 0.012     |
|                       |                          | $\psi$      | 0.222     | -0.47 | 39,325.2 | 0.076   | 0.089     | 0.370     |
|                       |                          | N           | 12.565    | -0.73 | 24,531.4 | 3.396   | 9.000     | 19.000    |
|                       |                          | D           | 0.004     | -     | -        | 0.001   | 0.003     | 0.006     |
|                       |                          | p           | 0.008     | -     | -        | 0.002   | 0.003     | 0.012     |
| Buffal<br>o<br>Valley | Blood<br>lure<br>cameras | N/A         | N/A       | N/A   | N/A      | N/A     | N/A       | N/A       |
|                       | All<br>cameras           | N/A         | N/A       | N/A   | N/A      | N/A     | N/A       | N/A       |

Table 3.4. Cougar density as estimated by CAPWIRE, comparing the equal catchability model (ECM) and two innate rates model (TIRM). Density was estimated using the ad hoc buffering method. Northwest Wyoming.

|      |     | Trap  | ECM   |       |          |         |       |          | TIRM  |       |          |         |       |          |
|------|-----|-------|-------|-------|----------|---------|-------|----------|-------|-------|----------|---------|-------|----------|
|      |     | area  | ECM   | CI95% | CI95%    | density | CI95% | CI95%    | TIRM  | CI95% | CI95%    | density | CI95% | CI95%    |
| 2013 | GV  | 816   | 30.00 | 23.00 | 39.00    | 3.68    | 2.82  | 4.78     | 45.00 | 35.00 | 73.00    | 5.51    | 4.29  | 8.95     |
|      | BV  | 648   | 11.00 | 6.00  | $\infty$ | 1.70    | 0.93  | $\infty$ | 18.00 | 7.00  | $\infty$ | 2.78    | 1.08  | $\infty$ |
|      | TSA | 1,401 | 38.00 | 29.00 | 50.00    | 2.71    | 2.07  | 3.57     | 55.00 | 42.00 | 89.00    | 3.93    | 3.00  | 6.35     |
| 2014 | GV  | 816   | 16.00 | 11.00 | 24       | 1.96    | 1.35  | 2.94     | 33.00 | 19.00 | 156      | 4.04    | 2.33  | 19.12    |
|      | BV  | 648   | 10.00 | 8.00  | 18       | 1.54    | 1.23  | 2.78     | 18.00 | 9.00  | 45       | 2.78    | 1.39  | 6.94     |
|      | TSA | 1,401 | 27.00 | 19.00 | 38       | 1.93    | 1.36  | 2.71     | 48.00 | 35.00 | 98       | 3.43    | 2.50  | 7.00     |

Table 3.5. AICc ranking for SECR models for cougar scat collection surveys in Northwest Wyoming, without sex grouping. x and y indicate a latitudinal or longitudinal gradient to density. ~1 indicates parameters that are held constant.

| Year | Area           | Model                         | K | logLik   | AICc    | dAICc  | AICcwt |
|------|----------------|-------------------------------|---|----------|---------|--------|--------|
| 2013 | Combined areas | D~x + y g <sub>0</sub> ~1 σ~1 | 5 | -198.889 | 410.506 | 0      | 0.653  |
|      |                | D~x g <sub>0</sub> ~1 σ~1     | 4 | -201.579 | 412.897 | 2.391  | 0.1976 |
|      |                | D~y g <sub>0</sub> ~1 σ~1     | 4 | -202.305 | 414.349 | 3.843  | 0.0956 |
|      |                | D~1 g <sub>0</sub> ~1 σ~1     | 3 | -204.249 | 415.498 | 4.992  | 0.0538 |
| 2013 | Gros Ventre    | D~1 g <sub>0</sub> ~1 σ~1     | 3 | -164.446 | 336.154 | 0      | 0.3806 |
|      |                | D~x g <sub>0</sub> ~1 σ~1     | 4 | -163.273 | 336.768 | 0.614  | 0.28   |
|      |                | D~y g <sub>0</sub> ~1 σ~1     | 4 | -163.288 | 336.799 | 0.645  | 0.2757 |
|      |                | D~x + y g <sub>0</sub> ~1 σ~1 | 5 | -163.099 | 339.728 | 3.574  | 0.0637 |
| 2014 | Combined areas | D~1 g <sub>0</sub> ~1 σ~1     | 3 | -125.071 | 257.988 | 0      | 0.7038 |
|      |                | D~y g <sub>0</sub> ~1 σ~1     | 4 | -124.855 | 261.044 | 3.056  | 0.1527 |
|      |                | D~x g <sub>0</sub> ~1 σ~1     | 4 | -125.065 | 261.464 | 3.476  | 0.1238 |
|      |                | D~x + y g <sub>0</sub> ~1 σ~1 | 5 | -124.842 | 265.139 | 7.151  | 0.0197 |
| 2014 | Gros Ventre    | D~1 g <sub>0</sub> ~1 σ~1     | 3 | -70.2986 | 151.397 | 0      | 0.9456 |
|      |                | D~x g <sub>0</sub> ~1 σ~1     | 4 | -70.2223 | 158.445 | 7.048  | 0.0279 |
|      |                | D~y g <sub>0</sub> ~1 σ~1     | 4 | -70.2704 | 158.541 | 7.144  | 0.0266 |
|      |                | D~x + y g <sub>0</sub> ~1 σ~1 | 5 | -69.9603 | 169.921 | 18.524 | 0      |
| 2014 | Buffalo Valley | D~1 g <sub>0</sub> ~1 σ~1     | 3 | -53.4806 | 118.961 | 0      | 0.9905 |
|      |                | D~x g <sub>0</sub> ~1 σ~1     | 4 | -53.4613 | 128.256 | 9.295  | 0.0095 |
|      |                | D~x + y g <sub>0</sub> ~1 σ~1 | 5 | -53.1118 | 146.224 | 27.263 | 0      |
|      |                | D~y g <sub>0</sub> ~1 σ~1     | 4 | -70.2704 | 158.541 | 39.58  | 0      |

Table 3.6. Population parameter estimates from top SECR models based on cougar scat collection (non-sex grouping models) in Northwest Wyoming. Data was not sufficient for the Buffalo Valley in 2013. Density estimates are in cougars per 100 km<sup>2</sup>.

Estimates for  $\sigma$  are in meters.

| Year | Area           | Top model    | Density | SE   | 95% CI         | G <sub>0</sub> | SE   | 95% CI        | $\sigma$ | SE    | 95% CI           |
|------|----------------|--------------|---------|------|----------------|----------------|------|---------------|----------|-------|------------------|
| 2013 | Combined area  | D ~ lat long | 2.19    | 1.01 | (0.92 - 5.19)  | 0.03           | 0.01 | (0.01 - 0.05) | 5,233    | 931   | (3,702 - 7,396)  |
|      | Gros Ventre    | null         | 5.70    | 2.25 | (2.70 - 12.02) | 0.03           | 0.01 | (0.01 - 0.04) | 4,409    | 1,054 | (2,777 - 7,000)  |
|      | Buffalo Valley | null         | -       | -    | -              | -              | -    | -             | -        | -     | -                |
| 2014 | Combined area  | null         | 2.62    | 0.97 | (1.30 - 5.28)  | 0.02           | 0.02 | (0.02 - 0.10) | 3,920    | 817   | (2,617 - 5,873)  |
|      | Gros Ventre    | null         | 2.98    | 1.60 | (1.11 - 8.00)  | 0.05           | 0.03 | (0.02 - 0.13) | 3,020    | 907   | (1,698 - 5,372)  |
|      | Buffalo Valley | null         | 1.94    | 1.71 | (0.44 - 8.56)  | 0.05           | 0.03 | (0.01 - 0.13) | 4,754    | 2,399 | (1,870 - 12,090) |

Table 3.7. AICc ranking for SECR models using genetics collected from cougar scat in Northwest Wyoming. Models incorporate a sex grouping (2014). ~g indicates a parameter with a group effect. x or y indicate a latitudinal or longitudinal gradient to the density estimate.

| Area           | model                | K | logLik   | AIC     | AICc    | dAICc  | AICcwt |
|----------------|----------------------|---|----------|---------|---------|--------|--------|
| Combined areas |                      |   |          |         |         |        |        |
|                | D~1 g0~1 σ~1         | 3 | -128.425 | 262.85  | 265.032 | 0      | 0.3249 |
|                | D~1 g0~g σ~1         | 4 | -126.909 | 261.819 | 265.819 | 0.787  | 0.2192 |
|                | D~+g g0~g σ~1        | 5 | -125.517 | 261.035 | 267.701 | 2.669  | 0.0856 |
|                | D~1 g0~g σ~g         | 5 | -125.905 | 261.81  | 268.477 | 3.445  | 0.058  |
|                | D~1 g0~1 σ~g         | 4 | -128.267 | 264.534 | 268.534 | 3.502  | 0.0564 |
|                | D~y g0~1 σ~1         | 4 | -128.356 | 264.712 | 268.712 | 3.68   | 0.0516 |
|                | D~x g0~1 σ~1         | 4 | -128.372 | 264.745 | 268.745 | 3.713  | 0.0508 |
|                | D~g g0~1 σ~1         | 4 | -128.392 | 264.783 | 268.783 | 3.751  | 0.0498 |
|                | D~y g0~g σ~1         | 5 | -126.839 | 263.679 | 270.345 | 5.313  | 0.0228 |
|                | D~x g0~g σ~1         | 5 | -126.864 | 263.728 | 270.395 | 5.363  | 0.0222 |
|                | D~1 + g g0~1 σ~g     | 5 | -127.716 | 265.432 | 272.099 | 7.067  | 0.0095 |
|                | D~y g0~1 σ~g         | 5 | -128.197 | 266.395 | 273.061 | 8.029  | 0.0059 |
|                | D~x g0~1 σ~g         | 5 | -128.211 | 266.422 | 273.089 | 8.057  | 0.0058 |
|                | D~x + y g0~1 σ~1     | 5 | -128.29  | 266.58  | 273.247 | 8.215  | 0.0053 |
|                | D~y + g g0~1 σ~1     | 5 | -128.323 | 266.645 | 273.312 | 8.28   | 0.0052 |
|                | D~x + g g0~1 σ~1     | 5 | -128.339 | 266.678 | 273.345 | 8.313  | 0.0051 |
|                | D~y + g g0~g σ~1     | 6 | -125.422 | 262.845 | 273.345 | 8.313  | 0.0051 |
|                | D~1 + g g0~g σ~g     | 6 | -125.423 | 262.847 | 273.347 | 8.315  | 0.0051 |
|                | D~x + g g0~g σ~1     | 6 | -125.452 | 262.903 | 273.403 | 8.371  | 0.0049 |
|                | D~y g0~g σ~g         | 6 | -125.82  | 263.641 | 274.141 | 9.109  | 0.0034 |
|                | D~x g0~g σ~g         | 6 | -125.856 | 263.712 | 274.212 | 9.18   | 0.0033 |
|                | D~x + y g0~g σ~1     | 6 | -126.782 | 265.563 | 276.063 | 11.031 | 0      |
|                | D~y + g g0~1 σ~g     | 6 | -127.641 | 267.283 | 277.783 | 12.751 | 0      |
|                | D~x + g g0~1 σ~g     | 6 | -127.645 | 267.29  | 277.79  | 12.758 | 0      |
|                | D~x + y g0~1 σ~g     | 6 | -128.128 | 268.255 | 278.755 | 13.723 | 0      |
|                | D~x + y + g g0~1 σ~1 | 6 | -128.257 | 268.513 | 279.013 | 13.981 | 0      |
| Gros Ventre    |                      |   |          |         |         |        |        |
|                | D~1 g0~1 σ~1         | 3 | -71.8947 | 149.789 | 155.789 | 0      | 0.9385 |
|                | D~1 g0~g σ~1         | 4 | -71.0782 | 150.156 | 163.49  | 7.701  | 0.02   |
|                | D~g g0~1 σ~1         | 4 | -71.642  | 151.284 | 164.617 | 8.828  | 0.0114 |
|                | D~1 g0~1 σ~g         | 4 | -71.6513 | 151.303 | 164.636 | 8.847  | 0.0113 |
|                | D~x g0~1 σ~1         | 4 | -71.7595 | 151.519 | 164.852 | 9.063  | 0.0101 |
|                | D~y g0~1 σ~1         | 4 | -71.8945 | 151.789 | 165.122 | 9.333  | 0.0088 |

|                   |                                   |   |          |         |         |        |        |
|-------------------|-----------------------------------|---|----------|---------|---------|--------|--------|
|                   | D~g g <sub>0</sub> ~l σ~g         | 5 | -68.6729 | 147.346 | 177.346 | 21.557 | 0      |
|                   | D~g g <sub>0</sub> ~g σ~l         | 5 | -69.3885 | 148.777 | 178.777 | 22.988 | 0      |
|                   | D~l g <sub>0</sub> ~g σ~g         | 5 | -70.3438 | 150.688 | 180.688 | 24.899 | 0      |
|                   | D~x g <sub>0</sub> ~g σ~l         | 5 | -70.9558 | 151.912 | 181.912 | 26.123 | 0      |
|                   | D~y g <sub>0</sub> ~g σ~l         | 5 | -71.068  | 152.136 | 182.136 | 26.347 | 0      |
|                   | D~x + g g <sub>0</sub> ~l σ~l     | 5 | -71.5069 | 153.014 | 183.014 | 27.225 | 0      |
|                   | D~x g <sub>0</sub> ~l σ~g         | 5 | -71.5258 | 153.052 | 183.052 | 27.263 | 0      |
|                   | D~x + y g <sub>0</sub> ~l σ~l     | 5 | -71.6329 | 153.266 | 183.266 | 27.477 | 0      |
|                   | D~y + g g <sub>0</sub> ~l σ~l     | 5 | -71.6419 | 153.284 | 183.284 | 27.495 | 0      |
|                   | D~y g <sub>0</sub> ~l σ~g         | 5 | -71.648  | 153.296 | 183.296 | 27.507 | 0      |
|                   | D~g g <sub>0</sub> ~g σ~g         | 6 | -68.3351 | 148.67  | 232.67  | 76.881 | 0      |
|                   | D~x + g g <sub>0</sub> ~l σ~g     | 6 | -68.5089 | 149.018 | 233.018 | 77.229 | 0      |
|                   | D~y + g g <sub>0</sub> ~l σ~g     | 6 | -68.6635 | 149.327 | 233.327 | 77.538 | 0      |
|                   | D~x + g g <sub>0</sub> ~g σ~l     | 6 | -69.2373 | 150.475 | 234.475 | 78.686 | 0      |
|                   | D~y + g g <sub>0</sub> ~g σ~l     | 6 | -69.3614 | 150.723 | 234.723 | 78.934 | 0      |
|                   | D~y g <sub>0</sub> ~g σ~g         | 6 | -70.0387 | 152.077 | 236.077 | 80.288 | 0      |
|                   | D~x g <sub>0</sub> ~g σ~g         | 6 | -70.1548 | 152.31  | 236.31  | 80.521 | 0      |
|                   | D~x + y g <sub>0</sub> ~g σ~l     | 6 | -70.7602 | 153.52  | 237.52  | 81.731 | 0      |
|                   | D~x + y + g g <sub>0</sub> ~l σ~l | 6 | -71.3802 | 154.76  | 238.76  | 82.971 | 0      |
|                   | D~x + y g <sub>0</sub> ~l σ~g     | 6 | -71.3895 | 154.779 | 238.779 | 82.99  | 0      |
| <hr/>             |                                   |   |          |         |         |        |        |
| Buffalo<br>Valley | D~l g <sub>0</sub> ~l σ~l         | 3 | -71.8947 | 149.789 | 155.789 | 0      | 0.9385 |
|                   | D~l g <sub>0</sub> ~g σ~l         | 4 | -71.0782 | 150.156 | 163.49  | 7.701  | 0.02   |
|                   | D~g g <sub>0</sub> ~l σ~l         | 4 | -71.642  | 151.284 | 164.617 | 8.828  | 0.0114 |
|                   | D~l g <sub>0</sub> ~l σ~g         | 4 | -71.6513 | 151.303 | 164.636 | 8.847  | 0.0113 |
|                   | D~x g <sub>0</sub> ~l σ~l         | 4 | -71.7595 | 151.519 | 164.852 | 9.063  | 0.0101 |
|                   | D~y g <sub>0</sub> ~l σ~l         | 4 | -71.8945 | 151.789 | 165.122 | 9.333  | 0.0088 |
|                   | D~g g <sub>0</sub> ~l σ~g         | 5 | -68.6729 | 147.346 | 177.346 | 21.557 | 0      |
|                   | D~g g <sub>0</sub> ~g σ~l         | 5 | -69.3885 | 148.777 | 178.777 | 22.988 | 0      |
|                   | D~l g <sub>0</sub> ~g σ~g         | 5 | -70.3438 | 150.688 | 180.688 | 24.899 | 0      |
|                   | D~x g <sub>0</sub> ~g σ~l         | 5 | -70.9558 | 151.912 | 181.912 | 26.123 | 0      |
|                   | D~y g <sub>0</sub> ~g σ~l         | 5 | -71.068  | 152.136 | 182.136 | 26.347 | 0      |
|                   | D~x + g g <sub>0</sub> ~l σ~l     | 5 | -71.5069 | 153.014 | 183.014 | 27.225 | 0      |
|                   | D~x g <sub>0</sub> ~l σ~g         | 5 | -71.5258 | 153.052 | 183.052 | 27.263 | 0      |
|                   | D~x + y g <sub>0</sub> ~l σ~l     | 5 | -71.6329 | 153.266 | 183.266 | 27.477 | 0      |
|                   | D~y + g g <sub>0</sub> ~l σ~l     | 5 | -71.6419 | 153.284 | 183.284 | 27.495 | 0      |
|                   | D~y g <sub>0</sub> ~l σ~g         | 5 | -71.648  | 153.296 | 183.296 | 27.507 | 0      |
|                   | D~g g <sub>0</sub> ~g σ~g         | 6 | -68.3351 | 148.67  | 232.67  | 76.881 | 0      |
|                   | D~x + g g <sub>0</sub> ~l σ~g     | 6 | -68.5089 | 149.018 | 233.018 | 77.229 | 0      |
|                   | D~y + g g <sub>0</sub> ~l σ~g     | 6 | -68.6635 | 149.327 | 233.327 | 77.538 | 0      |
|                   | D~x + g g <sub>0</sub> ~g σ~l     | 6 | -69.2373 | 150.475 | 234.475 | 78.686 | 0      |
|                   | D~y + g g <sub>0</sub> ~g σ~l     | 6 | -69.3614 | 150.723 | 234.723 | 78.934 | 0      |

|   |   |          |         |         |        |   |
|---|---|----------|---------|---------|--------|---|
| $D \sim y \, g_0 \sim g \, \sigma \sim g$         | 6 | -70.0387 | 152.077 | 236.077 | 80.288 | 0 |
| $D \sim x \, g_0 \sim g \, \sigma \sim g$         | 6 | -70.1548 | 152.31  | 236.31  | 80.521 | 0 |
| $D \sim x + y \, g_0 \sim g \, \sigma \sim 1$     | 6 | -70.7602 | 153.52  | 237.52  | 81.731 | 0 |
| $D \sim x + y + g \, g_0 \sim 1 \, \sigma \sim 1$ | 6 | -71.3802 | 154.76  | 238.76  | 82.971 | 0 |
| $D \sim x + y \, g_0 \sim 1 \, \sigma \sim g$     | 6 | -71.3895 | 154.779 | 238.779 | 82.99  | 0 |

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Table 3.8. Results from top ranked SECR models using genetics collected from cougar scat in Northwest Wyoming. Models incorporate a sex grouping (2014). The combined area model was a model average. Density estimates are in cougars per 100 km<sup>2</sup>.

Estimates for  $\sigma$  are in meters.

| Area           | Top model       | Sex     | Density | SE   | 95% CI        | G0   | SE   | 95% CI        | $\sigma$ | SE    | 95% CI           |
|----------------|-----------------|---------|---------|------|---------------|------|------|---------------|----------|-------|------------------|
| Combined area  | (null)+(g0~sex) | Males   | 1.09    | 0.40 | (0.54 - 2.2)  | 0.06 | 0.28 | (0.03 - 0.14) | 3,918    | 792   | (2,645 - 5,802)  |
|                |                 | Females | 1.09    | 0.40 | (0.54 - 2.2)  | 0.04 | 0.21 | (0.02 - 0.11) | 3,918    | 792   | (2,645 - 5,802)  |
| Gros Ventre    | null            | Males   | 1.22    | 0.66 | (0.04 - 3.30) | 0.05 | 0.03 | (0.02 - 0.15) | 3,012    | 901   | (1,698 - 5,345)  |
|                |                 | Females | 1.22    | 0.66 | (0.04 - 3.30) | 0.05 | 0.03 | (0.02 - 0.15) | 3,012    | 901   | (1,698 - 5,345)  |
| Buffalo Valley | null            | Males   | 0.73    | 0.78 | (0.13 - 4.05) | 0.05 | 0.03 | (0.02 - 0.14) | 5,081    | 2,957 | (1,762 - 14,646) |
|                |                 | Females | 0.73    | 0.78 | (0.13 - 4.05) | 0.05 | 0.03 | (0.02 - 0.14) | 5,081    | 2,957 | (1,762 - 14,646) |



Table 3.9. Density estimates for a population of cougars in Northwest Wyoming in cougars per 100 km<sup>2</sup>. Columns 1-3 compare camera trapping estimates to a telemetry-based reference estimate; Columns 4-6 compare scat collection estimates to the telemetry-based estimate after being adjusted to estimate additional non-adults. We did not estimate a reference or perform camera trapping in 2014; we did not collect scat in 2012. Other missing values are due to inadequate sample size.

| Year | Area           | Reference<br>est. | SPACECAP cameras<br>(95% HPD) | MARK cameras<br>(95% CI) | Adj. reference<br>est. | SECR scat<br>(95% CI) | CAPWIRE scat<br>(95% CI) |
|------|----------------|-------------------|-------------------------------|--------------------------|------------------------|-----------------------|--------------------------|
| 2012 | Gros Ventre    | 1.16              | 0.57 (0.4 - 0.9)              | -                        | 1.97                   | -                     | -                        |
|      | Buffalo Valley | 0.34              | -                             | -                        | 0.58                   | -                     | -                        |
|      | Combined areas | 0.91              | 0.57 (0.4 - 0.8)              | 0.21 (0.21 - 0.21)       | 1.55                   | -                     | -                        |
| 2013 | Gros Ventre    | 0.90              | 0.95 (0.4 - 0.8)              | -                        | 1.53                   | 5.70 (2.70 - 12.02)   | 3.44 (2.68 - 5.59)       |
|      | Buffalo Valley | 0.25              | -                             | -                        | 0.43                   | -                     | 1.74 (0.68 - ∞)          |
|      | Combined areas | 0.72              | 1.1 (0.7 - 1.6)               | 0.3 (0.3 - 0.3)          | 1.22                   | 2.19 (0.92 - 5.19)    | 2.46 (1.88 - 3.97)       |
| 2014 | Gros Ventre    | -                 | -                             | -                        | -                      | 2.98 (1.11 - 8.00)    | 4.04 (2.33 - 19.12)      |
|      | Buffalo Valley | -                 | -                             | -                        | -                      | 1.94 (0.44 - 8.56)    | 2.78 (1.39 - 6.94)       |
|      | Combined areas | -                 | -                             | -                        | -                      | 2.62 (1.30 - 5.28)    | 3.42 (2.56 - 7.00)       |

Table 3.10. Cost comparison for noninvasive survey methods used to determine population estimates of cougars, northwestern Wyoming.

| Survey Method | Equipment cost | Lab cost   | Fuel cost  | Personnel cost** | Total cost   | Number of detections | Person-days of effort | Detections per person-day | Cost per detection |
|---------------|----------------|------------|------------|------------------|--------------|----------------------|-----------------------|---------------------------|--------------------|
| Remote        |                |            |            |                  |              |                      |                       |                           |                    |
| Cameras       | \$57,770.00    | N/A        | \$4,200.00 | \$93,600.00      | \$155,570.00 | 48                   | 650                   | 0.0738                    | \$3,241.04         |
| Detection     |                |            |            |                  |              |                      |                       |                           |                    |
| Dogs          | N/A            | \$8,895.00 | N/A        | \$19,378.07      | \$28,273.07  | 83*                  | 40                    | 2.0750                    | \$340.64           |
| Winter        |                |            |            |                  |              |                      |                       |                           |                    |
| Transects     | N/A            | \$450.00   | \$260.64   | \$14,544.00      | \$15,254.64  | 2*                   | 101                   | 0.0198                    | \$7,627.32         |

\*Total detections used in analysis; does not include encounters that failed to yield a genetic identification (219 scat samples were collected from detection dogs ; 19 sets of tracks were encountered in winter transects)

\*\*Based on person-days of work at a wage of \$144 per day

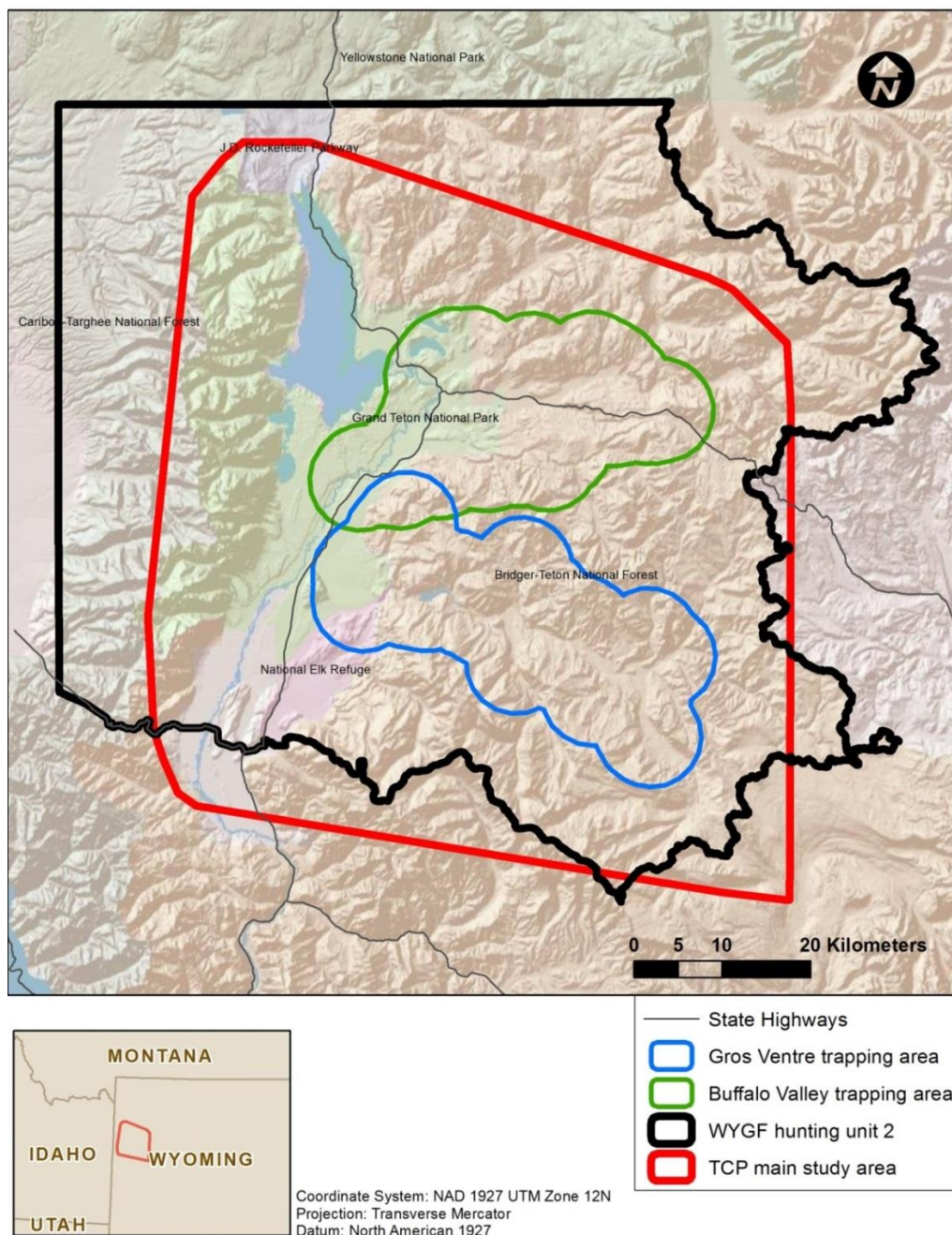


Figure 3.1. The study area, as defined by a minimum convex polygon of all recorded cougar locations over the course of the broader cougar ecology study (in red), northwestern Wyoming. The blue and green polygons delineate the area divisors for determination of the reference density.

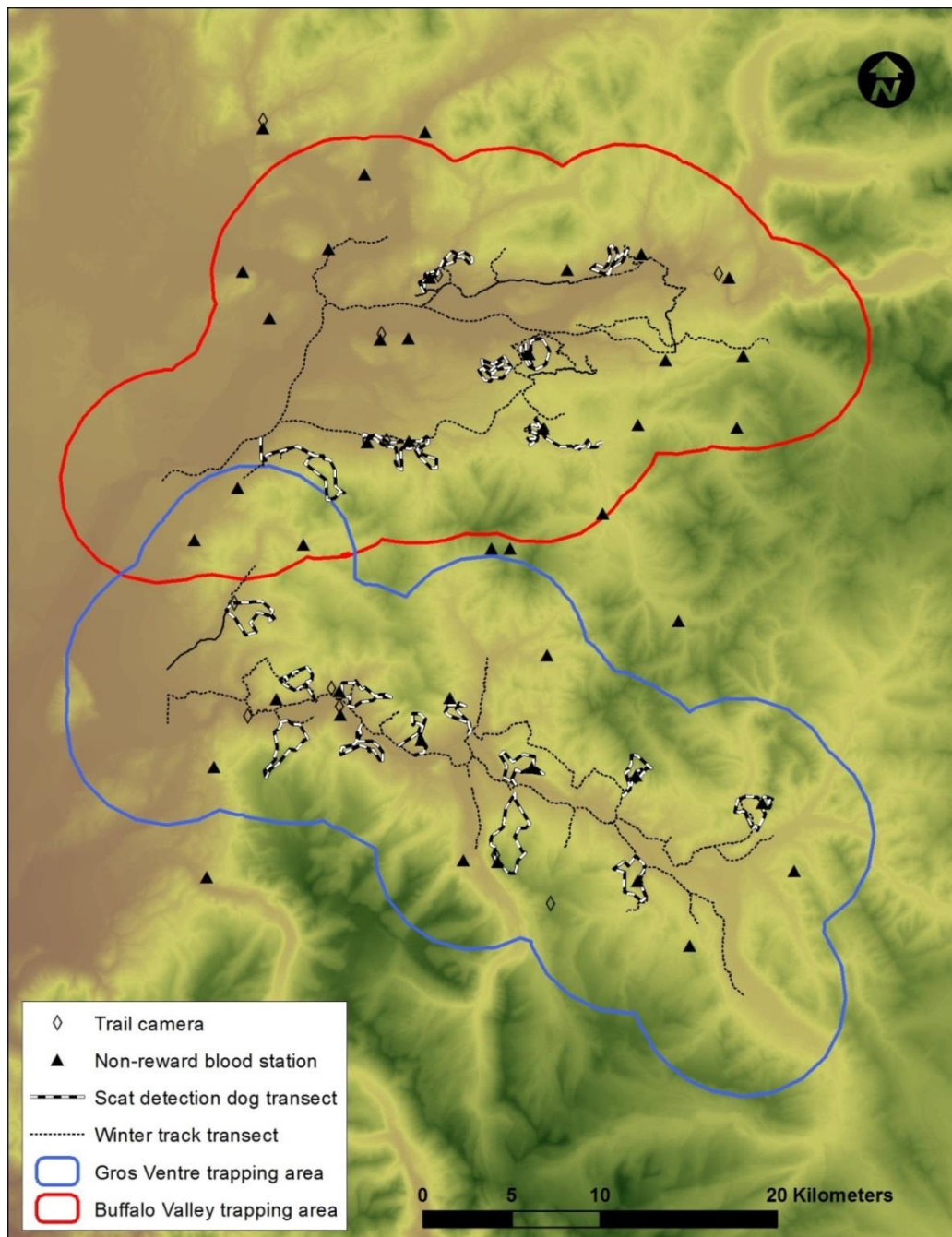


Figure 3.2. Locations of noninvasive detectors and the effective trapping area (area divisor) for detecting cougars, northwestern Wyoming.





Figure 3.3. An example of a photo detection of a cougar at a blood-lure station, northwestern Wyoming. This photo was one of several photos associated with this detection event.

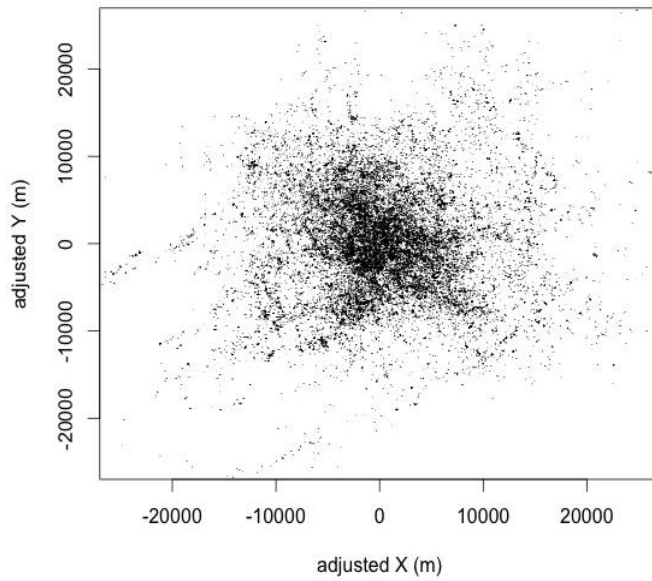


Figure 3.4. Multiple sets of cougar GPS locations, with each annual location set re-centered around the centroid of its respective home range, northwestern Wyoming.

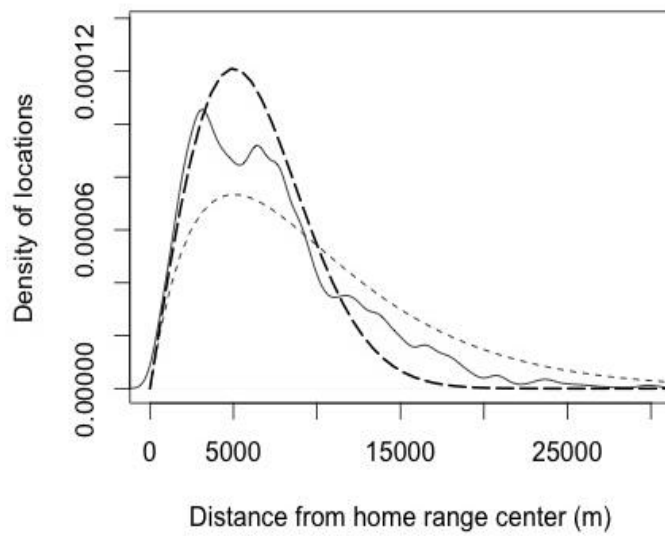




Figure 3.5. Density function for cougar GPS locations as a function of distance from individual home range center. The solid line represents the GPS locations. Heavy dashed line is a half-normal function. The light dashed line is the negative-exponential function.



File: C:\NIMP\NIMPyear2\photos\cataloged\Site218 pant41165 20  
Date/Time: 8/2/2012 12:22:50 AM  
Records: 4 of 28  
Event # 14  
Prev event Next event Site218  
8/2/2012 12:22:50 AM  
shorty  
Event Notes



File: C:\NIMP\NIMPyear2\photos\cataloged\Site211 cbs20\_2012-08  
Date/Time: 8/7/2012 6:44:34 PM  
Records: 7 of 15  
Event # 9  
Prev event Next event Site211  
8/7/2012 6:44:34 PM  
kelly  
Event Notes

5.76 days apart  
15.061 km apart  
study area map  
help

EventA 14 EventB 9 ID# 05  
Notes for this comparison  

check if same animal-----> ☐  
NOT same animal-> ☒  
Not able to tell ☐

Compile matched events into individuals  
Check for unmarked comparisons  
Export results to excel

Figure 3.6. A screenshot of the MS Access comparison form used to assess the agreement to which independent observers identified individual cougars photo-captured in northwest Wyoming. Users compared the two displayed events and assessed if the cougars were the same or different individuals.



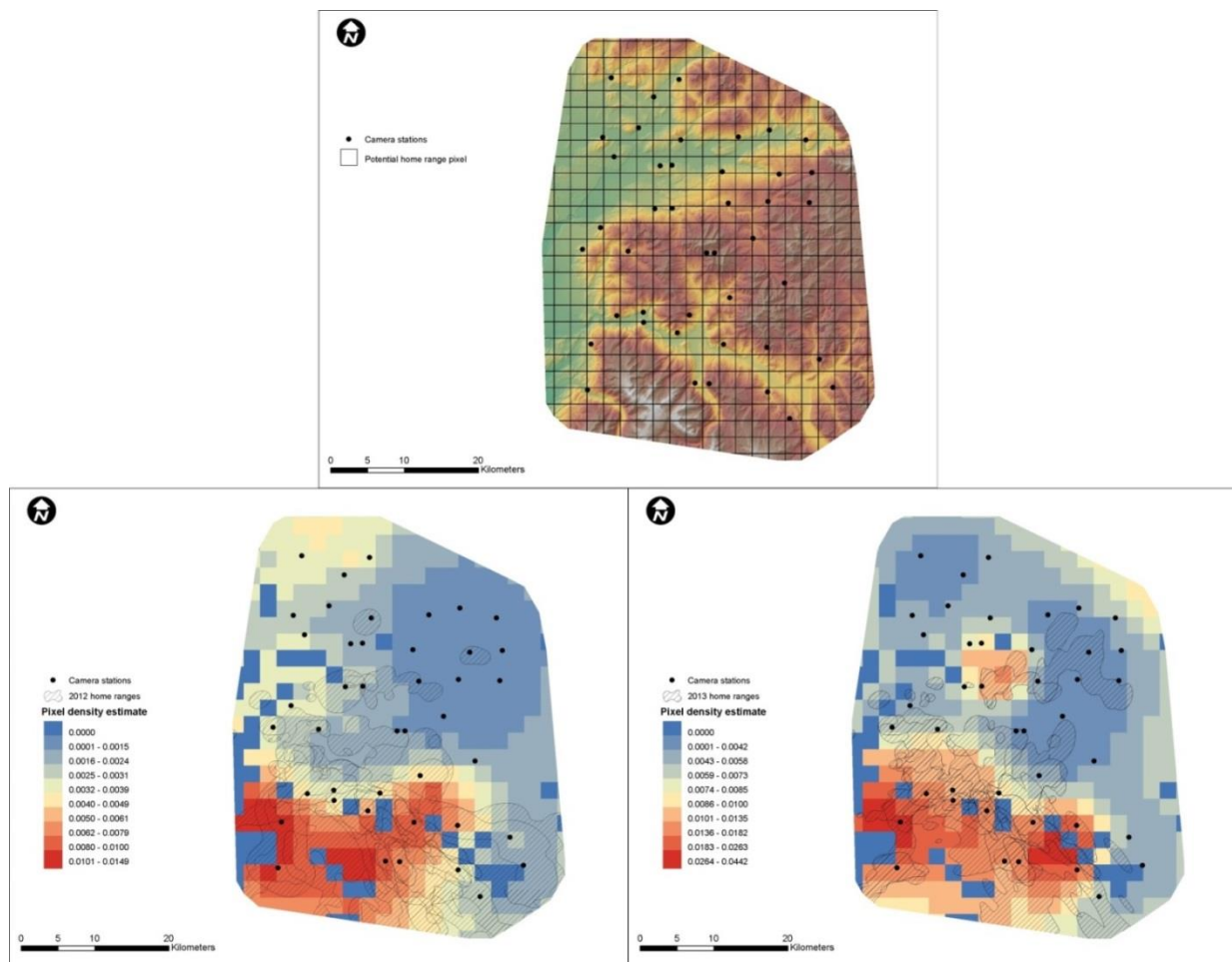


Figure 3.7. Maps with pixel density estimates for photo-captured cougars in northwest Wyoming, produced by SPACECAP. The top map displays the grid of empty 5 km<sup>2</sup> pixels representing potential home range centers. The bottom maps display 2012 and 2013 pixel density estimates, overlaid with home ranges derived from GPS telemetry.

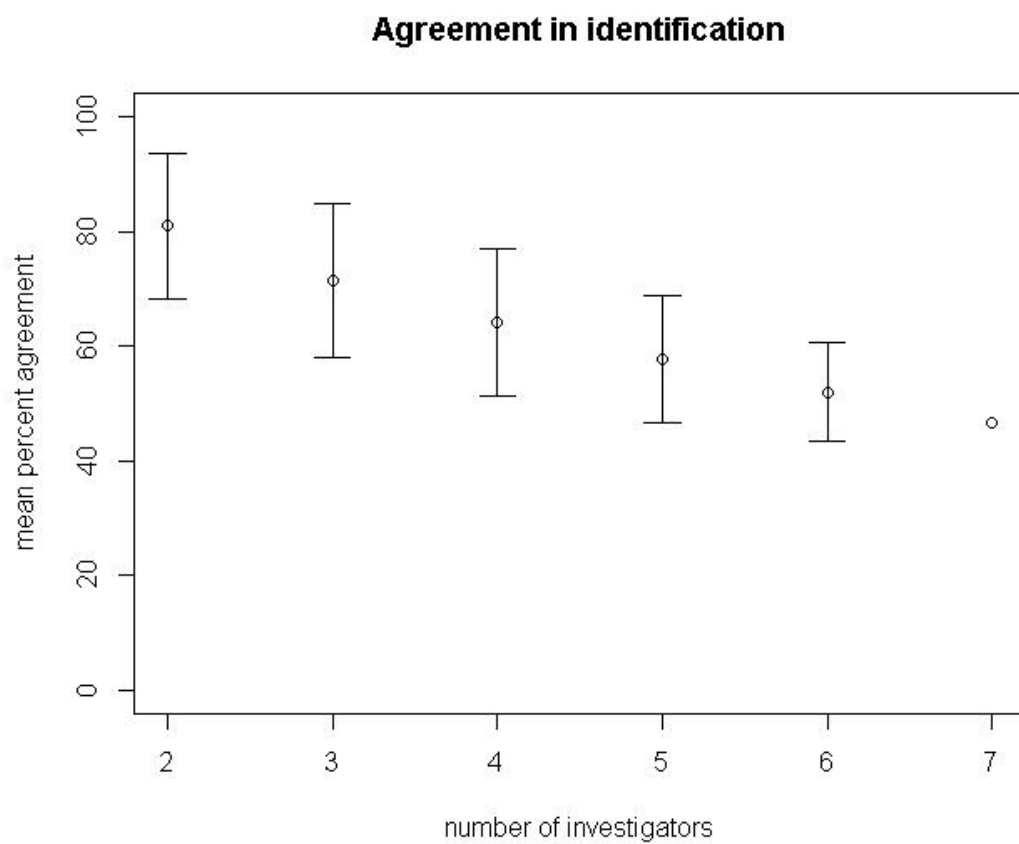


Figure 3.8. Percent agreement for identifying individual cougars from photographs as a function of the number of investigators queried; error bars indicate the standard deviation of the agreement level.

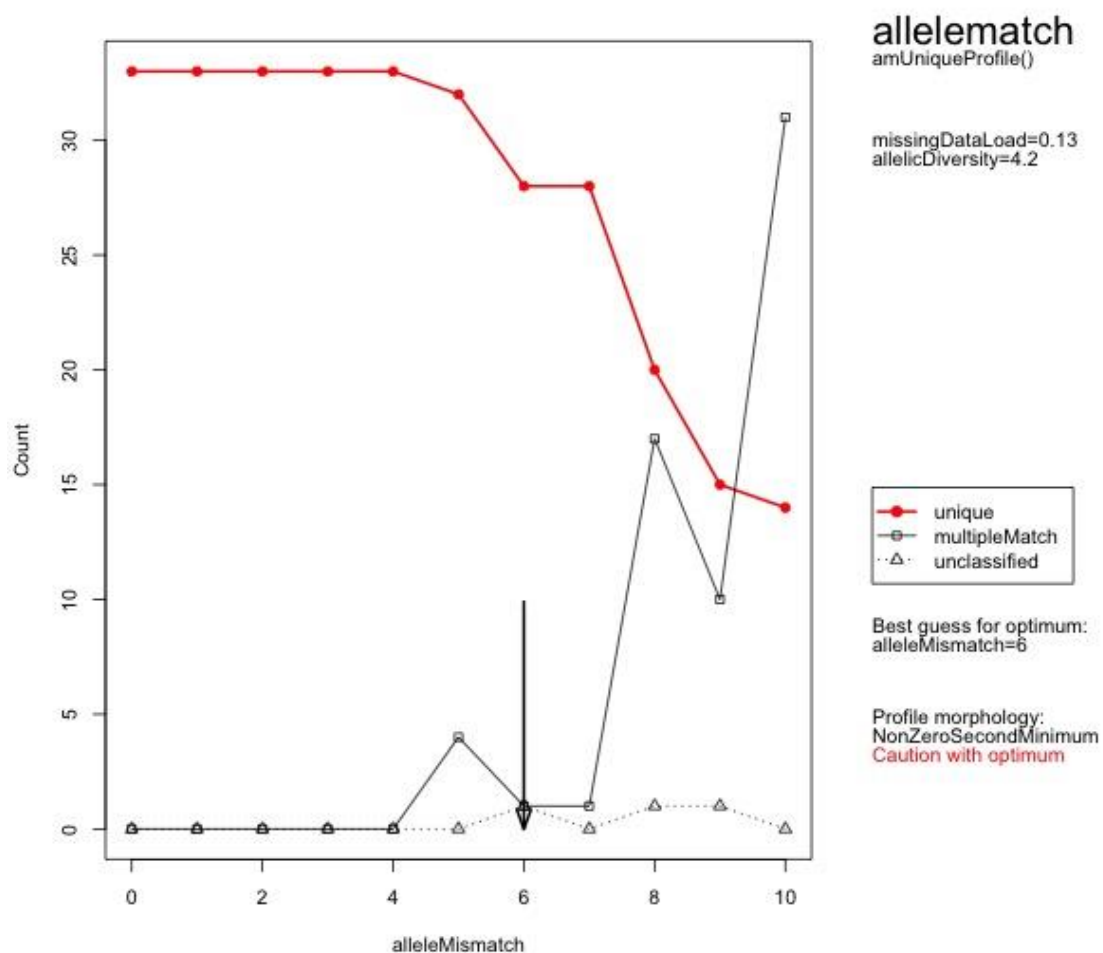


Figure 3.9. Output from the R package allelematch, indicating the optimum mismatch tolerance for determining matched genotypes of cougars sampled noninvasively by scat detection dogs in northwest Wyoming, 2013.

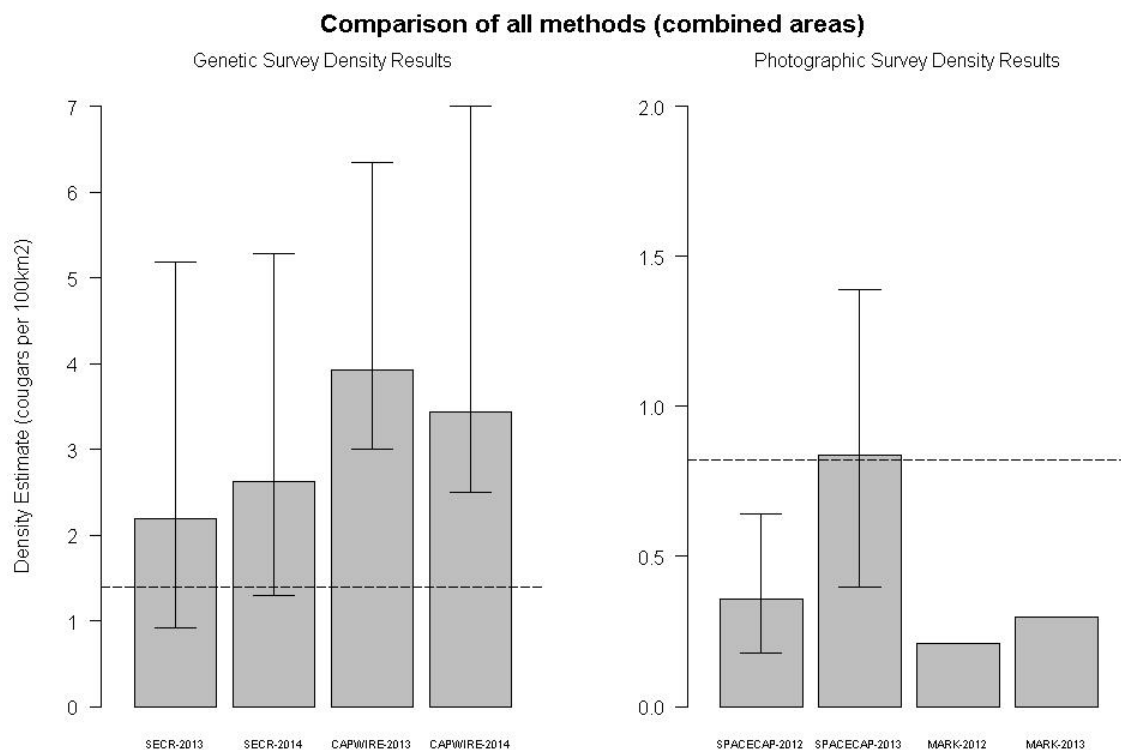


Figure 3.10. Yearly density estimates of cougars sampled noninvasively as determined by SECR, CAPWIRE, SPACECAP, and MARK in northwest Wyoming. The dotted line indicates the mean reference estimate (or adjusted mean reference estimate for genetic surveys), determined from 3 annual telemetry-based enumerations (2011 – 2013).

## CHAPTER 4

### CONCLUSIONS

This research should prove valuable to management and conservation entities responsible for monitoring cougar (*Puma concolor*) populations. In Chapter 2, we outlined the difficulties and biases associated with the “gold standard” methodology of determining cougar population size or density (i.e., capturing, collaring, and directly counting individuals; Cougar Management Guidelines Working Group 2005). Firstly, this research highlighted the potential for these capture based methods to underestimate cougar densities: acknowledging that different studies will have varying levels of capture effort and ability, our density estimates (for the combined area divisors) increased by an average of 65.2% ( $n = 3$ ) when including resident cougars that were detected by remote camera, but missed by capture efforts. Secondly, we argued that these enumerative methods should be used in conjunction with an area divisor (i.e., the area over which population size is divided to compute density) that is based on capture-effort (e.g., McLellan 1989) as opposed to animal location (e.g., Cooley et al. 2009a, b; Elbroch and Wittmer 2012). This method reduces bias associated with “cougar aggregations” (Smallwood 1997), and is more informative when making comparisons to other survey methods covering the same area. Using this method, we estimated the density of a population of cougars in Northwest Wyoming, which was spatially comparable to the noninvasive densities estimated in Chapter 3.

In Chapter 3, we examined three types of noninvasive survey methods to estimate cougar density: winter tracking transects, remote camera surveys, and scat detection dog surveys. Most importantly, our results demonstrated that scat detection dogs were an

order of magnitude less expensive than the other methods, in terms of cost-per-detection. The scat detection dog surveys also produced a greater number of detections in a shorter collection time, although the true sampling window (i.e., the temporal window in which an individual cougar could be detected) was not known with certainty. The winter tracking surveys did not yield enough detections for any useful population analysis; we recommend careful consideration of the issues outlined in our discussion, as well as similar studies' results (e.g., Sawaya et al. 2011, Russell et al. 2012). The remote camera survey produced fewer detections over a greater time span, and, most importantly, our analysis of human ability to identify individual cougars in photographs indicated that this method is not reliable in a capture-mark-recapture framework. We also demonstrated that SECR models (Efford 2011, Royle et al. 2011) may be more applicable to cougar populations than conventional CMR models, due to cougars' large home ranges that can extend beyond the boundaries of a survey area.

Cougars, as with many large carnivores, have undergone major population declines and range contractions over the past century due to habitat loss, habitat fragmentation, and direct human persecution (Ripple et al. 2014). In recent decades, many cougar populations have exhibited signs of recovery at local range levels (Thompson and Jenks 2010, LaRue et al. 2012, Knopff et al. 2014), while others may still be susceptible to decline (Laundre et al. 2007, Knopff et al. 2010). Given cougars' vast historic range, and potential role as both a top-down regulator (Ripple and Beschta 2006) and an umbrella species (Beier 2009), identifying these areas of extirpation or recolonization should be a priority for conservationists and managers. In this thesis, we learned important lessons on the applicability and efficacy of three commonly proposed

noninvasive survey techniques for cougars. We also addressed several issues and difficulties that can hamper monitoring efforts, including those related to cougars' large home ranges (i.e., temporary immigration/emigration; Kendall et al. 1997) and tendency to shift in population aggregations over time (Smallwood 1997).

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